CSIR

WNNR

FOR-DEA no : 393

To: DEPARTMENT OF WATER AFFAIRS AND FORESTRY

Contract : 1991/2

Project no. : 900-92065

Project title : St Lucia swamp forests

Deliverable no : 1

Deliverable title : The syntaxonomy and synecology of swamp forests in the Lake St Lucia area

Contact person : Mr D Owen

Division of Forest Science and Technology

Divisie vir Boskunde en -tegnologie

DELIVERABLE REPORT

ECOSYSTEMS MANAGEMENT PROGRAMME

Contract	:	DWAF
Project no	:	92065
Project title	:	St Lucia Swamp forests
Deliverable no	:	1
Deliverable title	:	The syntaxonomy and synecology of swamp forests in the Lake St Lucia area, Natal
Project leader	:	C J Geldenhuys
Project researcher	:	N G Wessels
DWAF contact person	:	Mr G H von dem Bussche
Date	:	November 1991
Notes	:	Report is prepared for publication by author, currently in the service of CPA Nature Conservation (Cedarberg)

Programme Manager

THE SYNTAXONOMY AND SYNECOLOGY OF SWAMP FORESTS IN THE LAKE ST LUCIA AREA, NATAL

N G Wessels

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N G Wessels

George, South Africa

November, 1991

CLASSIFICATION PAGE

TITLE: The syntaxonomy and synecology of swamp forests in the Lake St Lucia area, Natal

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AUTHOR: N G Wessels

REPORT NO: **DATE:** November 1991 **PAGES:**
ISBN No:

KEYWORDS: Classification, Diameter distribution, CANOCO, Lake St Lucia, Swamp forest, TWINSPAN

PROJECT NO: 92065
SPONSOR: Department of Water Affairs and Forestry

COPIES OF THIS REPORT ARE AVAILABLE FROM:

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Division of Forest Science and Technology
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Pretoria 0001
South Africa

PUBLISHED BY:

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CONTENTS

The syntaxonomy and synecology of swamp forests in the Lake St. Lucia area, Natal

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ABSTRACT

The swamp forests between Sodwana Bay and the Msunduze river were mapped. Selected swamp forests were classified using Two-Way Indicator Species Analysis (TWINSPAN). Two major communities, namely *Phoenix reclinata* - *Microsorium punctatum* forests and *Barringtonia racemosa* - *Nephrolepis bisserata* forests were identified. Analysis of diameter data showed that both communities have typical inverse-J diameter class distributions. However, *Voacanga thouarsii* is the only tree species which has a typical inverse-J diameter distribution in both communities. Vegetation-environment relationships were investigated using CANOCO. Three soil variables (pH, magnesium and organic content) and four water variables (pH, calcium, conductivity and pHc) account for some variation in the vegetation of the swamp forests.

UITTREKSEL

Moeraswoude tussen Sodwanabaai en die Msunduzerivier is gekarteer. Geselekteerde woude is deur middel van tweerigting indikatorspesie-analise (TWINSPAN) geklassifiseer. Twee gemeenskappe, naamlik *Phoenix reclinata* - *Microsorium punctatum* - *Protosparagus falcatus* woude en *Barringtonia racemosa* - *Nephrolepis biserrata* woude is geïdentifiseer. Beide die gemeenskappe toon die tipiese omgekeerde-J deursneeklasverdeling. *Voacanga thouarsii* is egter die enigste spesie in moeraswoude met so 'n verdeling. Verwantskappe tussen plantegroei en omgewing is ondersoek deur gebruik te maak van CANOCO. Drie grondveranderlikes (pH, magnesium en organiese inhoud) en vier waterveranderlikes (pH, kalsium, geleiding en pHc) is verantwoordelik vir sekere verskille in die plantegroei van moeraswoude.

Keywords: CANOCO; diameter distribution, Lake St. Lucia, Zululand; swamp forest; TWINSPAN

INTRODUCTION

Little has been published on the syntaxonomy and synecology of South African swamp forests. Available literature is almost entirely descriptive and regional in nature (Henkel *et al.* 1936; Huntley 1965; Kriel *et al* 1966; Tinley 1976; Begg 1980; Bruton 1980; Moll 1980; Cooper 1985). Swamp forest is the second rarest forest type in Natal, and indeed South Africa, having a total area of only 4843 hectares (Cooper 1985). Large areas of this forest type are threatened by agriculture and forestry, and possibly by the proposed dune mining on Eastern Shores of the Lake St. Lucia estuary. Cooper (1985) has therefore called for strict conservation status of the remaining forests.

Cooper (1985) suggests that South African swamp forests may perform an important sediment filtering role. No other values have been attributed to South African swamp forests. Studies in American bottomland hardwood forests (akin to African swamp forests) have indicated that these forests have many useful attributes. They support a high density and diversity of flora and fauna, help to protect the quality of water and habitat in downstream systems, and serve as flood water storage areas (Gosselink & Lee 1989). In the United States the most obvious harvestable resource in bottomland hardwood forests is the timber crop (Turner *et al.* 1981). In Florida, cypress swamps have been used as tertiary treatment centres for domestic waste waters since 1973 and are 60% more cost effective than conventional physical treatment plants (Maltby 1986).

A study was initiated in the swamp forests between Sodwana Bay and the Msunduze river in Zululand to provide much needed baseline data on the syntaxonomy and synecology of South African swamp forests. This paper reports on the mapping of the swamp forests, a hierarchical floristic classification of selected forests, demography and dynamics of the communities, and plant-site relationships.

STUDY AREA

The study area covers approximately 2960 km^2, from Sodwana Bay in the north to the Msunduze river in the south, and from the N2 Highway in the west to the coastal dunes in the east (between 27°33'and 28°30'S and 32°17' and 32°41'E). The detailed studies were confined to the swamp forests occurring along the streams meandering through the coastal plains on Eastern Shores, Nyalazi and Dukuduku State Forests (Figure 1).

The study area forms part of the Mozambique Coastal Plain which extends from Mtunzini in the south and broadens northward into Mozambique. The coastal plain is characterized by high dunes along the coast giving way inland to a series of lower dune ridges and slacks (Hobday 1965). The geology of the area has not been mapped in detail, but Lindley & Scott (1987) extrapolated the geology from geological sections at Richards Bay. The underlying formation is comprised of low permeability Cretaceous siltstones. The overlying formations are comprised of unconsolidated Pleistocene fine sand, with silt, clay and organic material of alluvial estuarine and aeolian origin. The Pleistocene deposits are covered by shallow Holocene sands (Hobday 1976).

Impeded drainage and poor aeration characterize the Sterkspruit, Valsrivier and Katspruit soil forms of the depressions and pans of the Nyalazi area (Jacobs *et al.* 1989). Fernwood (Warrington and Shasha series) or Champagne soil forms dominate the pans and depressions on Eastern Shores and have a relatively low organic carbon content (Schafer & Van Wyk 1988). Water tables were found to fluctuate to the surface of these soils and were recorded at depths of between 200 mm and 600 mm at the time of the survey. South of the Bhangazi pan an irregular sequence of fine sands, sandy loams and fine silty sands occur with discontinuous bands of peat and clay (Reid 1969). These layers may form impermeable layers resulting in perched water tables. An electrical sounding profile on Eastern Shores showed that immediately beneath the surface layer of dry sand, a water-bearing layer of sand overlies a clayey bedrock (Van Zijl 1971).

The area is part of the coastal lowland bioclimatic subregion (Phillips 1973; Taylor 1982) and transitional between the tropical and sub-tropical climatic regions (Stuckenburg 1969). The anti-cyclonic or orographic rainfall is influenced by the proximity of the sea and the topography of the land. It occurs in longitudinal zones with the highest isohyets along the coastal dunes, with a mean annual rainfall of 1157 mm at the estuary mouth and a decrease in a north-westerly direction to 623 mm in the northern section of False Bay (Venter 1979; Taylor 1980). The wettest months are January to April and the driest months July to September (Venter 1979; Jacobs *et al.* 1989).

At Charter's Creek weather station, the mean annual temperature to the west of the lake is 21.5° C. The highest monthly mean is 35.3° C in January and the lowest monthly mean 5.5° C in July (Taylor 1982; Jacobs *et al.* 1989). East of the lake, mean monthly maximum temperatures recorded at Cape St. Lucia range from 21.3°C to 28.5° C with extremes being moderated to some extent by the proximity of the sea and the warm Mozambique current (Taylor 1980).

METHODS

A stereoscope was used to map all swamp forests occurring between Sodwana Bay and the Msunduze river on 1:50 000 aerial photographs. Units were verified in the field as far as possible and their boundaries then copied onto 1:50 000 topocadastral maps. ARC/INFO GIS software (1990) was used to map swamp forest localities and to calculte their individual areas.

Only the swamp forests occurring on the Dukuduku, Nyalazi and Eastern Shores State Forests were sampled. These were randomly sampled to determine a broad classification of the different swamp forest communities. Twenty three circular plots of 400 m^2 were initially sampled. All plant species were recorded and three strata were recognized, a canopy layer, a shrub layer and a ground layer.

Trees and shrubs of over 5 m height, i.e. the canopy stratum, were recorded by DBH and species. Shrubs and saplings between 0,4 m and 5,0 m high, the shrub stratum, were recorded by number of plants (density). The ground layer (less than 0,4 m) was evaluated on a presence/absence (frequency) basis. Nomenclature follows Gibbs-Russell *et al.* (1985 & 1987). It was possible for a particular tree or shrub species, depending on its structural attributes, to be present in all three layers.

A standardized method was developed to enumerate *Ficus trichopoda*. This species has a peculiar growth form in that main branches have the tendency to grow horizontally and are supported by stilt-roots. These stilt-roots may eventually develop into separate trees, and it becomes difficult to identify the parent tree. For the purposes of this study, each vertical stem over 5 m high was considered to be a separate tree. Horizontal stems were disregarded. A number of other tree species occasionally develop multi-stems. Stems (> 5 m) of trees that were multi-stemmed below breast height (1,3 m), were measured and recorded separately.

The data set was classified using Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979). The density of stems per sample (canopy and shrub layers) and the presence or absence (frequency) of species in the ground layer was used for the input matrix. TWINSPAN is a computer programme developed essentially for analyzing data sets in which the frequencies of species have been recorded for a set of samples. The programme splits the samples into groups through a series of successive divisions. Using the groups of samples as a basis, the species are then classified according to their preferentiality to either side of a division. Several species may be identified as being particularly diagnostic of each division in the classification. The output is in the form of a two-way table that clearly demonstrates the association between species and samples (Hill 1979).

For the purposes of this study seven pseudospecies cut levels (levels of species' abundance) were used for the TWINSPAN classification, that is, 0-2, 2-5, 5-10, 10-20, 20-40, 40-80 and > 80. In this instance, pseudospecies 1 was a species occurring once in a plot, pseudospecies 2 had 2 to 4 stems in a plot, and pseudospecies 7 had 80 or more stems in a plot. Because the species in the ground layer were evaluated on a presence/absence basis, those present in a plot were assigned a value of 1.

On the basis of the preliminary classification, four broad swamp forest community types were randomly selected for sampling. Transects, two per broad community type, were placed across the width (i.e. across the drainage line) of each selected forest patch. Circular plots (400 m^2) were then sampled along the transects, wherever changes in floristic composition occurred. A total of forty plots were sampled, five to eight per transect, depending on the variability and size of the forest patch.

The final data set (63 plots) was classified using TWINSPAN. Species occurring less than three times in the data set were omitted. Sample plots 10, 17 and 27 were ommitted due to alien infestation and human disturbance (road-building and harvesting operations). The two-way table for this final classification was re-arranged so that species preferential to the same plots were grouped in descending order of abundance.

The demographic status of each of the communities identified by TWINSPAN, and of the ten most common tree species, was investigated. Using the DBH data, histograms indicating the stem density in seven diameter classes were produced. The diameter classes were: < 5 cm; 5-9 cm; 10-14 cm; 15-19 cm; 20-29 cm; 30-49 cm; and > 50 cm. A histogram for each community was produced using the DBH data of all tree species. For each of the ten tree species, a histogram was produced using their diameter class distributions in each of the communities.

Water and soil samples were collected for all transect plots, as well as for some which were close to the transects. In the centre of each plot, a fence auger (diameter of 25 cm) was used to bore a hole 1,2 m deep. Water samples (500 ml each) were collected 24 hours later, so as to allow for the settling of suspended sediments. The samples were collected 15 cm below the surface. The water samples were analyzed at the South African Sugar Association Experiment Station, Mt Edgecombe.

A bucket-type soil auger was used to collect soil from three different points in each of the above plots. Since it was difficult to discern distinct soil horizons in the swamp forests, soil samples were taken at two levels, from the top 15 cm and from below 1 m. For each plot, samples of 100 cm^3 were collected for both "horizons". The samples were analyzed for physical and chemical properties at the Saasveld Forestry Research Centre.

The relationships between the communities identified by TWINSPAN and the environmental variables, were investigated using the computer programme CANOCO (ter Braak 1986). This programme is a multivariate direct gradient analysis technique based on Canonical Correspondence Analysis. It identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that are best explained by the environmental variables.

A Student's t-test (PROC TTEST; SAS Institute Inc. 1990) was applied to the data to determine which soil and water variables were significantly different between the communities. Tukey's Honestly Significantly Difference (HSD) test was then applied to the data to determine which variables differentiated the sub-communities. This test was applied using PROC GLM implemented in the SAS/STAT software (SAS Institute Inc. 1990).

RESULTS AND DISCUSSION

Distribution

Figure 1 indicates the distribution of swamp forests in the study area. Swamp forests were easily identified on aerial photographs because they occur in drainage lines and can be differentiated from other forest types as physiognomically homogeneous units. The units on the Dukuduku, Nyalazi and Eastern Shores State Forests were visited. All were verified as swamp forests. Units north of Lake Bhangazi were not visited because of time constraints and inaccessibility.

Insert Figure 1

The total area of swamp forest in the study area is 3095 ha. This represents 64% (of a total of 4843 ha) of all swamp forests in Natal. The Mfabeni swamp forest on Eastern Shores State Forest covers an area of 352 hectares, and is therefore one of the largest individual swamp forests in South Africa. Many of the forests are however very small and isolated (less than 5 ha).

Composition

Eighty seven plant species were recorded in the sampled forests. Trees and shrubs are the most abundant life forms, making up 54% of the flora (47 species). Lianes and vines comprise 14,9% of the flora (13 species) and ferns 12,6% (11 species). Sixteen other herbaceous species were recorded. All species are listed in Table 1.

The swamp forests show considerable variation in composition. However, there are numerous species which appear to have a broad "ecological tolerance" and are quite common throughout the study area. The most common tree species is *Voacanga thouarsii* which is abundant in almost all the sampled forests . It occurs across the entire flood plain, from the less wet peripheries to the permanently inundated zones. *Syzygium cordatum* and *Ficus trichopoda* also occur in most of the sampled forests but are less abundant. *Macaranga capensis*, *Rapanea melanophloeos* and *Myrica serrata* would appear to be peripheral species but individuals may occur sporadically throughout the flood plain. *Ficus trichopoda* tends to grow along the main drainage channels, spreading outwards by means of horizontal branches. This species appears to regenerate entirely by vegetative means since no seedlings were ever observed.

The most commonly occurring shrub is *Psychotria capensis*. *Tarenna pavettoides* is abundant in most plots except those in which *Syzygium cordatum* is very abundant. Ferns make an important contribution to the shrub layer throughout the swamp forests. Eleven species, including the rare *Psilotum nudum*, were recorded. The most widespread species is *Stenochlaena tenuifolia*. *Nephrolepis biserrata* is abundant in most of the Eastern Shores plots but is rarely found in the Dukuduku swamp forests. In the northern part of the Mfabeni swamp forest *N. biserrata* forms impenetrable thickets, excluding to a large extent any regeneration. *Scleria angusta* is fairly common and occurs in canopy gaps where surface water is present.

Lianes and vines are an important constituent of the swamp forests, although only *Canthium gueinzii*, *Rhoicissus rhomboidea* and *Smilax kraussiana* occur throughout. The ground layer is poorly developed in all the forests, but is especially so in those in which *Barringtonia racemosa* and *Syzygium cordatum* are abundant. Plants comprising the ground layer are confined to the drier peripheries and islands. The ground layer is made up primarily by tree and shrub seedlings. The most commonly occurring seedlings are those of *Voacanga thouarsii*, *Barringtonia racemosa*, *Tarenna pavettoides* and *Psychotria capensis*. The few true herbs that do occur are found only on Dukuduku State Forest, in those forests where *Ficus trichopoda* is abundant.

Community classification

The classification of 60 sample plots is presented in Table 1. The dendrogram at the base of the two-way table indicates the levels of division and the indicator (in bold) and differential species for each community and sub-community. The values for each species denote categories of abundance defined by the seven pseudospecies cut levels.

Insert Table 1

The first division split the swamp forests into two main community types. The first community type (Community 1) is comprised of 23 plots, and has *Phoenix reclinata*, *Microsorium punctatum* and *Protosparagus falcatus* as its diagnostic species. All 23 plots are on the Dukuduku State Forest. The second main community type (Community 2) is comprised of 37 plots, and has

Barringtonia racemosa and *Nephrolepis biserrata* as its diagnostic species. This community is found mainly on the Eastern Shores State Forest, with a few, small, isolated patches on the Nyalazi State Forest.

On the second level of division, TWINSPAN split Community 1 into two sub-communities. The sub-community comprising 17 plots, has *Phoenix reclinata* as an indicator species. The other sub-community of 6 plots has no typical indicator species, but the absence of *Phoenix reclinata* differentiates this sub-community from the first. It is also characterized by the high pseudospecies values of *Voacanga thouarsii* and *Cassipourea gummiflua*, as well as by the differentiating presence of *Macaranga capensis*. However this division is not easily recognized in the field and the two sub-communities are therefore not discussed separately.

Community 2 was split into two sub-communities. A sub-community comprising 26 plots (2.1) has *Barringtonia racemosa* and *Tarenna pavettoides* as indicator species. The second sub-community comprising of 11 plots (2.2), is identified by the complete absence of *Barringtonia racemosa*. It has no typical indicator species, but is characterized by the high pseudospecies values of *Syzygium cordatum* and the differentiating presence of *Myrica serrata* and *Rapanea melanophloeos*. Further levels of division were ignored because only Community 1, and Community 2 and its two sub-communities, are easily recognised in the field.

Five species groups were identified. The species in group A are preferential to Community 1. Species in group B are preferential to both Community 1 and the *Barringtonia racemosa* - *Tarenna pavettoides* sub-community. Group C is comprised of species which are non-preferential. The species of group D are preferential to just the *Barringtonia racemosa* - *Tarenna pavettoides* sub-community. Although the species in group E are fairly common in all the forests, they are more preferential to sub-community 2.2.

Diameter class distribution

The distributions of stems over diameter classes for Community 1 and sub-communities 2.1 and 2.2 are presented as histograms (Figure 2). All have typical inverse-J diameter class distributions. The diameter class distributions for the ten most common tree species are presented in Figure 3. *Voacanga thouarsii* is the only species with a typical inverse-J diameter distribution in Community 1 and sub-communities 2.1 and 2.2. This species would therefore appear to have a broad ecological tolerance, since environmental variables within the three associations differ considerably (see community-environmental relationships). *Barringtonia racemosa* is absent from Community 1 and sub-community 2.2, but has an inverse-J diameter distribution in sub-community 2.1. In this sub-community, *B. racemosa* has a very large seedling/sapling bank. Its absence in the other two associations could be attributed to its dispersal strategy (see community descriptions). *Syzygium cordatum* has an inverse-J distribution in sub-community 2.2, but is poorly represented in Community 1 and sub-community 2.1. *S. cordatum* performs better than other species in sub-community 2.2, possibly indicating a greater tolerance of the highly acidic soils. *Ficus trichopoda* has a very irregular diameter class distribution in both communities. This may be attributed to the tendency of this species to regenerate apparently entirely by vegetative means. *Bridelia micrantha* performs better in Community 1 than in Community 2, perhaps indicating that the species prefers the less acidic conditions present in the former. In sub-community 2.1 *Bridelia micrantha* has a discrepancy in the smaller size classes. This would seem to indicate that *B. micrantha* became established, and still persists, but is unable to regenerate in this sub-community. The species may have established before *Barringtonia racemosa* became so dominant, but is now being competitively excluded. In sub-community 2.2, *B. micrantha* has regenerated abundantly, but there are very few mature trees. This does not indicate advanced regeneration because the canopy in this sub-community is discontinuous. Instead, it might indicate that conditions are too limiting for this species to develop to maturity. . *Macaranga capensis* performs better in sub-communities 2.1 and 2.2 than in Community 1. In both sub-communities it has an inverse-J diameter distribution, possibly indicating a moderate tolerance of the more acidic conditions. *Cassipourea gummiflua* has advanced regeneration in both communities, but is probably best represented in sub-community 2.2 because of the more open canopy. This species would appear to have a fair degree of ecological tolerance in the swamp forests since it has roughly inverse-J diameter class distributions in all three associations. *Rapanea melanophloeos* is poorly represented in Community 1 and sub-community 2.1, but has a large number of stems in the smaller diameter classes in sub-community 2.2. Generally a forest margin species, *R. melanophloeos* may have become established across the width of this sub-community in drier periods. Evidence of fire (the presence of charcoal within the soil profile of sub-community 2.2) in the forest indicates that in periods of possibly extreme drought, the ground layer may "dry up", allowing species intolerant of water-logged conditions to become established. When wetter conditions invariably return, these species may either die, or persist on drier "islands" within the forest. *Phoenix* *reclinata* regenerates abundantly in Community 1, and appears to be more tolerant of conditions in this community than in Community 2, where it is virtually absent. *Cussonia sphaerocephala* is well represented in Community 1, with a diameter distribution roughly resembling an inverse-J. It has an irregular diameter distribution in Community 2. It appears not to be regenerating in sub-community 2.1, and is only represented in the smallest diameter class in sub-community 2.2.

Insert figures 2 and 3

Community - environmental relationships

The results of the soil and water laboratory analyses are summarized in Tables 2 and 3. Tables 4 and 5 give the results of the Student's t-test which compared the soil and water variables between Community 1 and Community 2. The results of the Tukey's HSD tests which compared the variables between Community 1, sub-community 2.1 and 2.2, are given in Tables 6 and 7.

Insert tables 2, 3, 4, 5, 6 and 7

The solutions of the canonical correspondence analyses for the soil and water variables are displayed as ordination diagrams (Figure 4). For both the soil and water data sets, the plots have been separated by CANOCO into groups which conform with the communities identified by TWINSPAN. The lack of discrete clusters indicates that some degree of continuity exists between the communities. Axis 2 has, in both analyses, separated Community 1 from Community 2, whilst axis 1 has separated sub-community 2.1 from 2.2. Variables accounting for little variation have been excluded from the diagrams.

The greatest variation in the soil variable data set is along the first axis. pH (for both horizons) is most negatively correlated with axis 1 and accounts for most of the observed variation (Fig. 4). In edaphic terms, the soils in Community 1 are less acidic (mean pH of 4,53 in upper horizon) than those in Community 2 (mean pH of 3,56 in the upper horizon)(Table 4). Magnesium and organic carbon content (both in the lower horizons) are most positively correlated with axis 1. The soils of Community 2 generally have higher concentrations of magnesium and organic carbon (see Table 4).

Magnesium, in the upper horizon, accounts for much of the variation (negative correlation) along the second axis, with Community 2 having higher concentrations than Community 1. pH (of both horizons), is most positively correlated with axis 2. Sub-community 2.2 has more acidic soils (mean pH of 3,04), than sub-community 2.1 (mean pH of 3,79) (Table 6).

Insert figure 4

The greatest variation in the water variable data set is along axis 1. pHc is the variable most closely correlated (positively) with this first axis and accounts for most of the variation. pHc is a theoretical value defined as the pH of water in equilibrium with free calcium carbonate ($CaCo_3$). If the pHc is < 8,4 there is a tendency for $CaCo_3$ to precipitate and the sodium adsorption ratio (SAR) of the soil solution is increased. If the pHc is > 8,4 then the water will dissolve any free calcium in the soil and thus lower the SAR. This may explain the extremely high concentrations of calcium in most of the soils. The mean pHc value for Community 1 (8,170) is statistically significantly less than that of Community 2 (mean pHc value of 9,778). Correspondingly, Community 1 has higher concentrations of calcium.

Water pH is the variable most negatively correlated with axis 1. In edaphic terms the water in Community 2 is statistically significantly more acidic (mean pH of 5,8) than those in Community 1 (mean pH of 7,6) (Table 5).

Calcium and conductivity account for most of the variation along axis 2. The water of Community 1 has statistically higher calcium and conductivity values than Community 2 (Table 5). pHc is most negatively correlated with axis 2, with Community 1 (mean pHc value of 8,170), sub-community 2.1 (9,205) and sub-community 2.2 (11,040), all having statistically different values. The water in sub-community 2.2 (mean pH = 4,49) is more acidic than the water in sub-community 2.1 (mean pH = 6,39) (Table 7).

The soils variables, pH, magnesium and % organic carbon, and the water variables, pH, calcium, conductivity and pHc, can therefore be considered the most important of the measured environmental variables. All account for some variation in the vegetation of the swamp forests.

Community descriptions

1. The *Phoenix reclinata* - *Microsorium punctatum* community

This community type is found only to the west of Lake St. Lucia, and the units are generally smaller and more scattered than those in the east. The swamp forests in this area grow along narrow drainage lines 20 to 100 metres wide. The forests are inundated with slow flowing water after heavy rains, the floodwaters draining in a haphazard, braid-like fashion across the floodplain. In the intervals between flooding, the forest floor is a mosaic of stagnant pools, sluggish streamlets and small islands.

The tree stratum is continuous and relatively low, not exceeding 12 m. The understorey usually consists of a dense entanglement of *F. trichopoda* horizontal branches and stilt roots, *Phoenix reclinata* shrubs, ferns and creepers. The soil is generally sand or sandy loam with a moderate percentage of organic matter (mean of 7,1 %) (Table 2). The soil is acidic, having a pH range 2.47 to 5.92 and mean of 4,5. Calcium concentrations are very high with a mean of 2452,4 ppm. The water in this community is generally alkaline with a pH range of 6,3 to 8,4 with a mean of 7,6. The water is minerally rich with high calcium, magnesium, and conductivity values (Table 3).

The indicator species for this community are *Phoenix reclinata, Microsorium punctatum* and *Protosparagus falcatus*. However in the field this community can more easily be recognized by a well developed canopy dominated by *Ficus trichopoda*. There is also a greater diversity of species in this community than in Community 2. Eighty one plant species were recorded for Community 1 (see Table 1). The species in species group A are preferential to this community. Apart from the diagnostic *Phoenix reclinata*, other preferential tree species include *Schefflera umbellifera, Scolopia zeyheri, Ilex mitis* and *Trichilia dregeana*. *Voacanga thouarsii* and *Bridelia micrantha* are also common components of the canopy.

The fern *Microsorium punctatum* is a diagnostic species in the shrub layer of this community. True shrub species that are preferential are *Kraussia floribunda* and *Bersama lucens*. The understorey shrub layer is, however, dominated by *Tarenna pavettoides*. *Psychotria capensis* is also abundant in most of the plots. *Protosparagus falcatus*, a creeper, is another diagnostic species for this community. There are three other preferential creeper species, *Mikania* *natalensis*, *Rhus nebulosa* and *Urera cameroonensis*.

The ground layer is poorly developed but is represented by a greater number of species than in Community 2. *Crassocephalum crepidioides* and a species of *Plectranthus* were found only in this community. The herbaceous layer consists mainly of the seedlings of *V. thouarsii*, *B. micrantha* and *T. pavettoides*. Two orchids, *Cyrtorchis arcuata* and *Eulophia horsfallii* were recorded only in this community. The two sub-communities cannot be differentiated in the field and have therefore not been discussed.

2. The *Barringtonia racemosa* - *Nephrolepis biserrata* community

This community type is found mainly to the east of Lake St. Lucia, with a few isolated patches occurring on the Nyalazi State forest. The two indicators species are *Barringtonia racemosa* and the fern *Nephrolepis biserrata*. This community type, which comprises 37 plots, was split by TWINSPAN into two sub-communities: a *Barringtonia racemosa* - *Tarenna pavettoides* sub-community comprising 26 plots, and a *Syzygium cordatum* sub-community comprising 11 plots. Although *Barringtonia racemosa* is an indicator species for Community 2 as a whole, it does not occur at all in the *Syzygium cordatum* sub-community. Both sub-communities can be differentiated in the swamp forest adjacent to the Mfabeni swamps (on Eastern Shores State forest). The southern part of this forest is a *Barringtonia racemosa* - *Tarenna pavettoides* sub-community, and the northern part is a *Syzygium cordatum* sub-community. The transition between the two sub-communities is abrupt, and could be attributed to the dispersal strategy of *Barringtonia racemosa*. The fibrous fruits, which are relatively large (6 x 4 cm), are buoyant and thus best dispersed by water (personal observation). This could in part explain why the southern (downstream) part of this forest is completely dominated by *B. racemosa*, whilst in the northern (or upstream) part, this species is completely absent. Because of the dissimilarity between the two sub-communities in the field, Community 2 as a whole is not discussed, and instead the two sub-communities are addressed separately.

2.1 The *Barringtonia racemosa* - *Tarenna pavettoides* sub-community

The best example of this sub-community type is the southern part of the Mfabeni swamp forest.

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Table 1. TWINSPAN table for the classification of swamp forest communities in the Lake St. Lucia area, Natal. In the list of species, "c" denotes tree and shrub species over 5 m in height, "j" denotes saplings and shrubs between 0.4 m and 5 m, "r" denotes seedlings, "s" denotes shrubs less than 0,4 m height, "v" denotes vines and lianes, "f" denotes ferns, and "h" denotes other herbaceous species. Some tree and shrub species appear three times, depending on their structural attributes. The localities of the plots are indicated by a "D", "N" or an "E" for Dukuduku, Nyalazi or Eastern Shores State Forest. Plots on transects are indicated by a number between 1 and 8, whilst "#" indicates plots not occurring on transects. The values for each species denote categories of abundance defined by the seven pseudospecies cut levels: 1 = 0-1; 2 = 2-4; 3 = 5-9; 4 = 10-19; 5 = 20-39; 6 = 40-79; 7 = > 80. "-" indicates the absence of a species. The dendrogram at the base of the table shows the levels of division and the indicator (in bold) or preferential species for each community and sub-community. Species occurring less than three times in the data set are listed below the table.

Community no.	1		2	
Sub-community no/	1.1	1.2	2.1	2.2
Plots	22 563456	233 1333 123333 80117942582393467	11111122244444444445345256 81265890140123457890968290	25556566555 31232413567
Locality	DDDDDD	DDDDNDDDDDDDDDDDD	NNENNEEEEEEEEEEEEEEEEEEEEE	EEEEEEEEEEE
Transect	###222	111####3441313344	#####5####5555556666567877	86887877888
SPECIES GROUP A				
Phoenix reclinata (c)	------	126-2-2---5434345	------------------------3-	-----------
Phoenix reclinata (j)	------	45465246265355433	---------------------1--2-	-----------
Microsorium punctatum (f)	1-11-1	-111111-111111111	11--------11--------------	-----------
Protasparagus falcatus (v)	111111	11-1111111-1-1211	111-1----11---------------	-----------
Kraussia floribunda (j)	--2---	2443221121515-2--	---------1-----------1----	-----------
Mikania natalensis (v)	11111-	11111111-11111111	1111--1---1-1--------11-1-	-----------
Rhus nebulosa (v)	-11-1-	1111111111111----	---1--------------------11	------1----
Urera cameroonensis (v)	--1111	-----11-1--111111	----------1------1------1-	-----------
Trichilia dregeana (c)	1--213	---1------1--11--	-------1------------------	-----------
Trichilia dregeana (j)	2-5356	-213---1-----1---	------------------1-------	-----------
Schefflera umbellifera (j)	---21-	--32-24-1512---22	-2--1---------------------	-----------
Schefflera umbellifera (c)	---24-	--21---21522---22	----3---------------------	-----------
Crassocephalum crepidioides (h)	-11-1-	1111111-1---11-1-	--------------------------	-----------
Phoenix reclinata (r)	--1---	11-1--111111111--	--------11--------------11	-----------
Allophyllus dregeanus (r)	--11--	11-1---1111--1-1-	---------1-1--11--------1-	-1---------
Scolopia zeyheri (j)	---12-	---2--1-14-2-1--1	--------------------------	-----------
Bersama lucens (j)	--2--1	-334-----1121-2-2	---------1---1-----------2	-----------
Ilex mitis (c)	---2--	-22---1--14-11--2	--------------------------	-----------
Bridelia micrantha (j)	-3-32-	-122-2142--------	1-------------------12----	--1-1---41-
Cussonia sphaerocephala (j)	---333	--22--2---41-1---	----21-----1----2---------	------2----
Apodytes dimidiata (j)	--3-2-	---321-----1----1	--------------------------	------12---
Flagellaria guineensis (v)	11111-	---1-------------	--------------------------	-----------
Plectranthus spp. (h)	1---11	-111------1-1----	--------------------------	-----------
Phragmites australis (h)	-1----	-1-----1---------	--------------------------	-----------
Eulophia horsfallii (h)	--111-	--1------1----11-	--------------------------	-----------
Rhus chirindensis (j)	---11-	-----1-----------	--------------------------	-----------
Harpephyllum caffrum (j)	----2-	-1----1----------	--------------------------	-----------
Bersama lucens (r)	--11--	-11------1----1-1	------------1-------------	-----------
Ficus natalensis (j)	2111--	--12------1-2--2-	---------------------1----	------1----
Apodytes dimidiata (c)	-2----	2112--------1---2	--------------------------	------1----
Scutia myrtina (r)	---1--	1--11-1-11-1-1---	--------------------------	-----------
Argyrolobium rupestre (h)	11-111	---1-1-1-1-------	1-------------------11----	-----------
Halleria lucida (j)	---111	----11--1------2-	-----------------------1--	-----------
Cyrtorchis arcuata (h)	---1--	-11------11-1---1	-1---1----1--1------------	-----------
Ilex mitis (j)	----2-	-24---1---2----1-	------------------------1-	-----------
Kraussia floribunda (c)	------	1-32------1-2----	--------------------------	-----------
Scolopia zeyheri (c)	------	---1-----2---2---	--------------------------	-----------
Bersama lucens (c)	------	--11-----1-1--1-1	--------------------------	-----------
Scutia myrtina (s)	------	---1-21-2------1-	--------------------------	-----------
Canthium inerme (j)	2-----	------1-------2--	--------------------------	-----------
Scadoxis multiflorus (h)	---1--	--11------1------	--------------------------	-----------
Trichilia dregeana (r)	----1-	-1----1----------	--------------------------	-----------
Schefflera umbellifera (r)	----1-	--1---1-1---1--11	--------------------------	-----------
Kraussia floribunda (r)	------	--11-1----1-1----	--------------------------	1----------
Myrica serrata (r)	------	1-1----1---------	--------------------------	-----------
Allophyllus dregeanus (c)	------	---------2--11--1	-----------1-1-----------1	-----------
Macaranga capensis (r)	---1--	--1----1------1--	---1----------1-----------	-----------
Burchellia bubalina (r)	----1-	------------1----	--------1-----------------	-----------

SPECIES GROUP B

Tarenna pavettoides (c)	4-6545	52342-55563442434	234-544125365556-323534434	---2-------
Tarenna pavettoides (j)	626746	53462264555554445	245-4452255554662432545354	211---41--1
Bridelia micrantha (c)	432-22	33143-34332111-2-	33-3132--12222221---224--3	-112------2
Allophyllus dregeanus (j)	--1-1-	5-64-154255254322	-----221132333-2----43--25	-1--1------
Cussonia sphaerocephala (c)	--4444	-123---1-212-1-22	--3123-----31321-------11-	------1----
Ficus sur (c)	-23--3	---33-23122-1-12-	1----32----32221-----12-12	-----------
Tarenna pavettoides (r)	111111	--1-111--1111-111	1111111-11111111--1-1-1111	-1--1------
Bridelia micrantha (r)	2-111-	--111111-111---1-	11-1-11----1111-----1-1---	-----11-1--
Ficus sur (j)	1--113	1-23312--12----2-	1----32----1-11-------3112	-----------
Oplismenus hirtellus (h)	11--1-	-1--1----1-------	---1-----1----1-----------	-----------
Rhoicissus tomentosa (v)	111-11	---1-1-----------	-1--1---1--111------------	-----------
Peddiea africana (j)	43--12	1----------------	3-11------------------2---	-----------
Thelypteris interrupta (f)	11-11-	-1-111111--------	1-11-------11---------1---	-1----11-1-
Cyperus spp. (h)	---1--	----1--11--------	---1---------------1-1---	------1-1--
Rauvolfia412Xcaff(e)	-3----	----------------1	1--------2-1-22-----------	-----------
Burchellia bubalina (c)	---2--	1----------------	------12--11-------1-----1	-----------
Halleria lucida (c)	----2-	-------1---------	---------2----3-----------	-----------
Asplenium prionitis (f)	-----1	-----------------	-----------1-1------------	-----------
Ficus sur (r)	------	-----1-----------	-----1-----1--------------	-----------
Psychotria capensis (c)	------	-------1------22-	-------1-----3-----1---1-1	--1--------
Rauvolfia caffra (j)	-2----	------1----------	--1-----------2---------1-	-----------
Sapium ellipticum (j)	2-11--	-----------------	-1-----------------2-----	--------1--
Peddiea africana (r)	1----1	-----------------	1-1-----------------------	-----------
Dalbergia armata (v)	-1----	-----------------	1-1-----------------------	-----------

SPECIES GROUP C

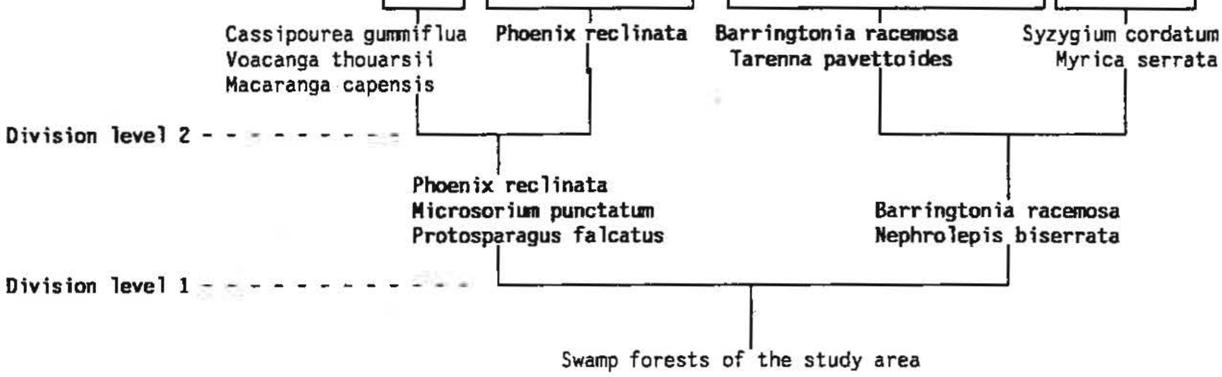
Voacanga thouarsii (c)	5524--	21341261324254554	32221444523443344435555254	224456551-2
Voacanga thouarsii (j)	666622	3336232542314122-	-525413442314--34343234132	225344564-3
Ficus trichopoda (c)	354-41	-43-563464-3-4655	12--21233241213-4442222-41	-31---651-2
Psychotria capensis (j)	--4335	36542435424655531	-14-3653354666662545662556	262-23551-1
Canthium gueinzii (v)	11-111	1-1111111111-1111	11111111111111111111111111	-11111-11-1
Cassipourea gummiflua (j)	--4555	3-2----2--2313---	114-31-12-1322113442121112	122122322-1
Rhoicissus rhomboidea (v)	1-1111	1111--11-1-111---	-1---11111-11111-11111-111	111-1111---
Stenochlaena tenuifolia (f)	111111	---11-1---1------	1111-111111-111111111111-1	11111111111
Microsorium scolopendrium (f)	---111	-11-1111-11111111	11-----11---1-11--11-1-1--	-1-111111-1
Psychotria capensis (r)	--1111	11-1-1112-111-11-	-11--1--11-1-111-1-11-1111	-1--11---1-
Syzygium cordatum (r)	-1-111	1-211-------1----	1111-1--------1-----1---1-	--1-1------
Smilax kraussiana (v)	----11	11111-11-11---1--	1-111-111----11-1---1-11-1	111111-111-
Macaranga capensis (c)	414-34	43--4--3-1-------	342-4----2-12122-22-465424	3442212----
Cassipourea gummiflua (c)	--1543	2-1---------12---	------1212---1-22222-4-323	-23-1522---
Macaranga capensis (j)	2-2132	212----2---------	-----------22-4-1--1244---	-5--1-1----
Voacanga thouarsii (r)	111111	---111111111-1111	11111-11----------1----111	--1-11-1---
Rapanea melanophloeos (r)	------	--11--111--1--1-1	------------1--1---1--1---	1-1---11111
Scleria angusta (h)	1--1--	--111-----1-1----	11111-111---111111-1111-11	-1--1-111-1
Landolphia petersiana (v)	1---1-	1111-1111111--11-	-11-----1----------111-1-1	11-1--11---
Ipomoea spp. (v)	11----	---1--11---------	-11-1---11----1-1--1111--1	111111-----
Ficus trichopoda (j)	-52---	--1----1--13-222-	--------2-----1-1---1-3-2-	-11--1----2
Antidesma venosum (c)	----2-	-----------------	---------3----1------2----	-1---------
Lindsaea ensifolia (f)	---1--	--1--------------	------------------11-1----	----1-11---
Psilotum nudum (f)	------	--1--------------	------------1--1---1------	------1----

SPECIES GROUP D

Barringtonia racemosa (c)	------	-----------------	7657566675676656655671----	-----------
Barringtonia racemosa (j)	------	-----------------	7777676777777676777775----	-----------
Barringtonia racemosa (r)	------	-----------------	111111-11-111--1111111----	-----------
Nephrolepis biserrata (f)	-----1	------1----------	-1--11-11--111111111-11111	1-11111----
Burchellia bubalina (j)	---12-	1-21-------31-21-	-----343323332-3211424--13	-1----2----
Sapium ellipticum (c)	--1--1	------------1----	-1-------1---232---22131-2	212-2-----2
Canavallia rosea (v)	------	-----------------	-----1---11-1-11----111--1	-1---------
Mimusops obovata (c)	------	-----------------	-----------121---2-123--1-	----1-1----
Mimusops obovata (j)	------	-----------1-----	-----21-1--342--322234---3	----1--1---
Lygodium microphyllum (f)	------	-----------------	----1---1-1--1-------1--1-	-----11----
Ficus natalensis (c)	------	-----------------	-1------11----------------	-----------
Cassipourea gummiflua (r)	------	-----------------	-------------------11---1	--1---1----
Sphagnum spp. (h)	------	-----------------	--------------------------	--------111
Nymphaea capensis (h)	------	-----------------	1-------------------------	----1-11--1

SPECIES GROUP E

Syzygium cordatum (c)	21-2--	-3433-23--4241121	11-222224-1--2124122335434	33465545777
Syzygium cordatum (j)	23-322	144-1211-21-311-1	-4252-----1-2--212-2245-23	-26-4443774
Rapanea melanophloeos (c)	----1-	1521---31---2-111	-----2--1-----2-1--14132--	162621226-5
Rapanea melanophloeos (j)	------	3544--1243-1--12-	----11----1---1-1--3442-1-	-6222332254
Myrica serrata (c)	------	241--------------	--------------------------	1----1142-5
Myrica serrata (j)	------	564--------------	-------------------1-1--	-----235535
38X	000000 000000	00000000000000000 11111111111111111	11111111111111111111111111 00000000000000000000000000	11111111111 1111111111



Sapium integerrimum; Psydrax obovata; Grewia caffra; Albizia adianthifolia; Celtis africana; Chaetacme aristata; Hymenocardia ulmoides; Eugenia capensis subsp. natalitia; Trimeria grandifolia; Brachylaena discolor; Clerodendrum glabrum; Strelitzia nicolai; Ficus vericulosa; Pteris vittata; Cheilanthes viridis; Centella asiatica; Issoglossa woodii; Scleria poaeformis; Schoenoplectus erectus.

Table 2. Chemical and physical properties of soils sampled in selected swamp forests of the Lake St. Lucia area, Natal. Two samples were collected in each plot: one from the top 15 cm, and the other from below 1 m. The first line for each plot indicates the properties of the top horizon, whilst the second line indicates the properties of the lower horizon.

Community	Plot	P(ppm)	K(ppm)	Ca(ppm)	Mg(ppm)	Al(ppm)	pH(KCl)	%organic	Soil type
1	1	3.67	131.0	4176.0	525.0	2.0	4.74	8.45	sandy clay loam
		0.60	8.0	381.0	29.0	2.0	5.13	8.23	
1	2	3.45	52.0	1904.0	222.0	0.0	4.82	3.09	sandy clay loam
		1.14	17.0	811.0	38.0	0.0	5.54	0.70	
1	3	10.07	86.0	700.0	382.0	32.0	4.24	3.57	sand
		0.63	7.0	65.0	10.0	5.0	4.36	0.18	
1	4	7.56	56.0	1150.0	296.0	63.0	4.14	5.37	organic matter
		2.86	48.0	1039.0	614.0	49.0	4.16	3.78	
1	6	6.51	86.0	944.0	76.0	27.0	4.05	6.53	sandy loam
		1.90	16.0	114.0	77.0	13.0	4.07	0.25	
1	7	4.41	43.0	2992.0	412.0	270.0	2.96	5.96	loamy sand
		2.82	14.0	779.0	76.0	29.0	3.72	0.83	
1	13	5.20	239.0	4210.0	123.0	2.0	4.70	10.19	sand
		1.51	6.0	603.0	67.0	409.0	2.47	1.01	
1	25	1.74	25.0	65.0	23.0	97.0	3.94	1.77	sand
		0.65	4.0	18.0	14.0	104.0	3.24	0.19	
1	26	8.97	90.0	791.0	552.0	139.0	3.61	5.78	sand
		0.46	7.0	368.0	123.0	4.0	4.35	0.31	
1	28	3.20	62.0	1846.0	412.0	0.0	5.36	5.31	sand
		0.86	13.0	440.0	21.0	0.0	5.92	0.43	
1	29	5.91	224.0	4683.0	923.0	0.0	5.05	10.14	sand
		0.67	8.0	746.0	16.0	52.0	2.92	0.81	
1	30	5.20	60.0	1800.0	328.0	0.0	5.97	3.10	loamy sand
		1.12	7.0	371.0	20.0	0.0	5.50	0.18	
1	31	5.21	222.0	4285.0	777.0	0.0	4.72	13.18	sandy loam
		1.24	13.0	746.0	48.0	0.0	5.80	0.36	
1	32	1.82	38.0	1110.0	253.0	0.0	4.78	1.69	sandy loam
		0.54	9.0	256.0	10.0	58.0	4.67	0.21	
1	33	5.08	145.0	2395.0	871.0	5.0	4.37	12.46	organic matter
		2.27	46.0	3349.0	558.0	2.0	4.65	6.03	
1	34	5.30	333.0	1698.0	1198.0	0.0	4.11	12.67	clay
		1.86	76.0	3284.0	684.0	2.0	5.42	0.73	
1	35	2.00	18.0	2588.0	435.0	0.0	4.89	3.36	sandy clay loam
		1.47	29.0	2457.0	354.0	4.0	4.41	1.45	
1	36	6.51	582.0	5204.0	936.0	9.0	4.54	12.88	clay
		1.59	67.0	4618.0	719.0	0.0	4.88	3.17	
1	37	6.51	1355.0	3580.0	1112.0	0.0	4.34	12.38	organic matter
		1.01	61.0	4299.0	700.0	0.0	4.74	6.27	
1	38	3.75	105.0	2926.0	646.0	0.0	5.30	3.77	sandy loam
		1.94	14.0	915.0	229.0	0.0	4.94	0.14	
2.1	8	7.55	42.0	168.0	121.0	122.0	3.86	2.07	loam
		1.96	16.0	241.0	135.0	45.0	3.84	0.63	
2.1	11	0.54	48.0	729.0	454.0	522.0	3.50	27.00	loamy sand
		1.15	3.0	96.0	25.0	27.0	3.85	0.67	
2.1	12	1.36	30.0	1729.0	959.0	23.0	3.78	9.42	sand
		0.74	6.0	223.0	72.0	97.0	3.10	1.15	
2.1	15	3.91	53.0	2090.0	270.0	104.0	3.48	14.82	sand
		6.23	54.0	2549.0	444.0	4.0	4.74	9.12	
2.1	16	4.07	78.0	336.0	351.0	162.0	3.71	3.40	sandy loam
		0.97	32.0	372.0	73.0	266.0	3.33	0.92	
2.1	18	12.35	212.0	2028.0	895.0	0.0	4.24	9.27	sandy loam
		0.77	17.0	180.0	38.0	0.0	5.46	8.20	
2.1	22	2.34	374.0	312.0	1211.0	173.0	2.90	27.00	sand
		2.18	4.0	0.0	2.0	34.0	4.41	0.60	
2.1	39	7.83	244.0	687.0	657.0	81.0	3.35	10.89	sandy loam
		1.24	36.0	319.0	106.0	22.0	4.14	1.50	
2.1	40	5.52	218.0	3263.0	991.0	4.0	4.35	7.50	sand
		1.01	22.0	208.0	98.0	4.0	4.29	1.72	
2.1	41	0.83	328.0	4469.0	1533.0	4.0	4.34	12.84	sandy loam
		1.94	48.0	858.0	111.0	4.0	4.28	1.16	
2.1	42	3.65	473.0	6117.0	1442.0	7.0	4.80	11.34	sandy loam
		1.12	20.0	230.0	58.0	4.0	4.16	0.51	
2.1	43	2.06	66.0	3677.0	874.0	5.0	4.25	9.85	loamy sand
		0.89	47.0	230.0	43.0	0.0	4.85	0.33	

Table 2 Continued

Community	Plot	P(ppm)	K(ppm)	Ca(ppm)	Mg(ppm)	Al(ppm)	pH(KCl)	%organic	Soil type
2.1	44	8.42	285.0	570.0	712.0	0.0	3.63	9.44	sand
		1.43	11.0	31.0	9.0	121.0	3.65	0.72	
2.1	45	3.72	308.0	1079.0	1195.0	0.0	4.19	11.12	loamy sand
		0.77	32.0	123.0	81.0	31.0	3.93	0.80	
2.1	46	2.00	216.0	2600.0	1653.0	0.0	3.20	13.94	organic matter
		0.67	27.0	126.0	707.0	54.0	3.87	3.22	
2.1	47	2.00	450.0	3097.0	2244.0	14.0	3.50	27.00	organic matter
		0.67	246.0	2510.0	1824.0	18.0	3.60	15.08	
2.1	48	1.58	203.0	1921.0	1149.0	14.0	3.62	11.52	organic matter
		2.75	100.0	1700.0	1150.0	18.0	3.70	14.75	
2.1	49	1.45	311.0	3097.0	2170.0	11.0	3.80	14.86	organic matter
		2.63	30.0	1657.0	1192.0	18.0	3.98	10.28	
2.1	50	6.29	111.0	1729.0	1252.0	74.0	3.90	11.67	loamy sand
		1.40	23.0	124.0	83.0	29.0	4.14	1.76	
2.1	58	9.04	312.0	650.0	1159.0	79.0	3.58	27.00	sand
		0.63	4.0	42.0	25.0	14.0	4.04	0.57	
2.1	59	5.20	404.0	3577.0	1544.0	5.0	3.86	14.16	organic matter
		0.35	43.0	5275.0	851.0	0.0	4.89	13.73	
2.1	60	4.96	391.0	2749.0	982.0	32.0	3.60	13.65	sand
		0.37	4.0	56.0	23.0	0.0	4.65	0.13	
2.2	51	8.70	169.0	575.0	490.0	23.0	3.38	12.75	sand
		1.47	7.0	15.0	9.0	14.0	4.47	0.11	
2.2	52	4.39	23.0	16.0	138.0	149.0	2.95	5.98	sand
		3.27	3.0	0.0	0.0	32.0	3.79	1.08	
2.2	53	1.70	169.0	402.0	500.0	112.0	2.37	15.00	organic matter
		0.76	60.0	344.0	2073.0	137.0	2.53	10.80	
2.2	54	1.70	367.0	1187.0	1582.0	83.0	2.50	15.12	organic matter
		0.89	65.0	3292.0	2277.0	83.0	2.81	13.92	
2.2	55	1.70	67.0	2000.0	1500.0	65.0	2.70	15.00	organic matter
		1.13	60.0	2360.0	707.0	65.0	2.64	14.28	
2.2	56	2.07	78.0	4733.0	705.0	20.0	2.51	12.53	organic matter
		0.41	37.0	1668.0	2367.0	34.0	2.81	12.91	
2.2	57	2.00	21.0	1222.0	1322.0	65.0	2.63	14.77	organic matter
		4.88	47.0	2421.0	1055.0	65.0	2.80	13.05	
2.2	61	1.46	284.0	2751.0	1679.0	0.0	4.00	27.00	organic matter
		0.54	51.0	2421.0	1058.0	2.0	4.33	12.55	
2.2	62	3.00	722.0	435.0	467.0	47.0	3.88	27.00	organic matter
		1.84	77.0	1393.0	1467.0	27.0	2.86	27.00	
2.2	63	1.43	126.0	3755.0	952.0	43.0	3.50	27.00	organic matter
		1.55	36.0	4562.0	2800.0	25.0	3.62	13.26	

Table 3. Chemical properties of water samples collected from selected swamp forests in the Lake St. Lucia area, Natal. All variables, except pH, EC (ohms), and pHc, are measured in milli-equivalents.

Community	Plot	pH	K	Ca	Mg	Na	Cl	SO_4	EC	pHc
1	1	8.4	0.8	2.4	0.7	1.8	2.8	0.1	46.0	7.7
1	2	8.4	0.5	3.0	0.8	3.0	4.2	0.1	66.0	7.5
1	3	7.5	0.0	0.5	0.5	1.9	2.7	0.2	30.0	9.0
1	4	7.5	0.0	1.0	0.4	2.0	2.8	0.2	32.0	8.9
1	6	7.3	1.0	0.6	0.4	2.6	3.3	0.3	38.0	9.0
1	7	8.3	0.8	1.5	0.8	2.0	2.3	0.9	47.0	7.9
1	13	8.3	0.0	1.8	0.7	1.7	2.3	0.2	38.0	7.9
1	25	6.3	0.0	0.4	0.4	1.1	1.3	0.3	16.0	9.6
1	26	6.6	0.0	0.4	0.3	1.1	1.0	0.6	18.0	9.6
1	28	8.5	0.7	0.6	0.7	2.3	2.5	0.2	50.0	7.9
1	29	8.4	0.6	0.5	0.5	1.5	1.8	0.2	42.0	8.1
1	30	8.2	0.6	2.2	0.9	2.8	4.8	0.2	63.0	7.8
1	31	8.3	0.6	2.4	0.8	1.9	2.6	0.2	49.0	7.6
1	32	7.9	0.0	0.9	0.4	1.4	1.8	0.2	27.0	8.4
1	33	8.4	0.0	2.4	0.8	2.1	2.8	0.2	48.0	7.7
1	34	8.3	0.0	2.1	0.8	2.2	2.7	0.2	46.0	7.7
1	35	8.1	0.9	2.3	0.7	2.2	2.9	1.5	52.0	8.0
1	36	8.4	1.0	2.6	0.9	2.2	3.0	0.2	54.0	7.5
1	37	8.4	0.9	2.4	0.9	2.2	3.1	0.2	53.0	7.6
1	38	8.0	0.9	1.1	2.9	7.7	5.5	8.1	130.0	8.0
2.1	8	4.9	0.8	0.7	0.8	2.2	2.5	1.7	43.0	9.3
2.1	11	4.1	0.0	2.1	2.6	3.6	6.2	5.4	8.0	11.2
2.1	12	7.3	0.0	0.5	0.5	1.9	2.6	0.2	30.0	9.0
2.1	15	4.6	0.0	0.5	0.7	3.1	4.1	0.7	48.0	9.4
2.1	16	7.6	0.8	0.8	0.7	1.6	1.8	6.9	29.0	8.8
2.1	18	0.8	1.0	0.8	0.3	1.1	1.1	0.2	20.0	8.4
2.1	22	6.9	0.9	0.3	0.1	0.4	0.4	0.2	5.0	12.1
2.1	39	7.4	1.0	0.6	0.4	1.7	2.1	0.1	25.0	9.0
2.1	40	7.5	1.1	1.1	0.3	1.0	1.3	0.2	16.0	8.5
2.1	41	8.1	0.9	1.1	0.3	1.2	1.3	0.2	24.0	8.2
2.1	42	7.4	1.1	0.6	0.3	1.3	1.6	0.2	20.0	9.0
2.1	43	7.6	0.7	0.6	0.4	1.5	1.9	0.2	24.0	8.8
2.1	44	7.8	0.8	0.5	0.3	1.8	1.8	0.1	24.0	8.7
2.1	45	6.2	0.4	0.4	0.1	0.6	0.6	0.2	7.0	9.7
2.1	46	7.7	0.7	0.5	0.4	1.5	1.8	0.2	23.0	8.8
2.1	47	6.6	0.7	0.8	0.3	1.3	1.7	0.1	21.0	9.1
2.1	48	5.3	0.6	0.4	0.3	1.5	1.8	0.1	21.0	9.3
2.1	49	5.4	0.3	0.7	0.4	1.4	1.9	0.1	21.0	9.1
2.1	50	5.5	0.0	0.8	0.4	1.5	1.9	0.1	22.0	9.1
2.1	58	6.8	0.0	0.4	0.3	1.2	1.5	0.4	17.0	9.6
2.1	59	7.7	0.0	0.6	0.4	1.3	1.5	0.2	21.0	8.6
2.1	60	7.4	0.0	0.8	0.4	1.6	1.8	0.1	23.0	8.8
2.2	51	7.1	0.0	0.4	0.5	2.2	2.7	0.4	31.0	9.2
2.2	52	4.1	1.0	0.3	0.3	1.1	1.5	0.3	20.0	12.0
2.2	53	4.1	1.2	0.4	0.4	1.4	1.8	0.2	25.0	11.9
2.2	54	4.1	1.2	0.5	0.4	1.6	2.0	0.1	26.0	11.8
2.2	55	3.9	0.9	0.6	0.6	2.4	3.2	0.2	40.0	11.7
2.2	56	3.8	0.3	0.5	0.7	2.7	3.4	0.2	44.0	11.7
2.2	57	4.1	0.0	0.6	0.8	3.0	3.9	0.1	49.0	11.7
2.2	61	4.9	0.0	0.5	0.4	1.3	1.7	0.1	20.0	9.5
2.2	62	3.9	0.0	0.4	0.5	2.0	2.6	0.2	33.0	11.8
2.2	63	4.9	0.0	0.7	0.4	1.6	0.8	0.1	22.0	9.1

Table 4a. Results of Student's t-test for comparison of soil variables (upper horizon) between Community 1 and Community 2.

Variable	P		K		Ca		Mg		Al		pH		% organic	
Community	1	2	1	2	1	2	1	2	1	2	1	2	1	2
N	20	32	20	32	20	32	20	32	20	32	20	32	20	32
Mean	5,104	3,900	197,60	224,46	2452,4	1992,2	525,10	1036,0	32,30	63,84	4,532	3,558	7,082	14,75
Std Error	0,499	0,519	67,88	29,08	76,94	96,85	76,94	96,85	15,10	17,37	0,148	0,106	0,911	1,291
Variances	Equal		Unequal		Equal		Unequal		Equal		Equal		Unequal	
T	1,5678		-0,3638		1,0574		-4,1306		-1,2594		5,4696		-4,8491	
DF	50,0		26,1		50,0		50,0		50,0		50,0		49,5	
Prob>[T]	0,1232		0,7189		0,2954		0,0001		0,2137		0,0000		0,0001	

Table 4b. Results of Student's t-test for comparison of soil variables (lower horizon) between Community 1 and Community 2.

Variable	P		K		Ca		Mg		Al		pH		%organic	
Community	1	2	1	2	1	2	1	2	1	2	1	2	1	2
N	20	32	20	32	20	32	20	32	20	32	20	32	20	32
Mean	1,357	1,519	23,500	39,625	1282,9	1113,3	220,35	655,09	36,65	40,44	4,545	3,861	1,763	6,453
Std Error	0,164	0,123	5,1003	7,8789	249,41	325,60	60,855	147,74	20,57	9,561	0,209	0,128	0,542	1,228
Variances	Unequal		Unequal		Equal		Unequal		Unequal		Equal		Unequal	
T	-0,5770		-1,7180		0,4167		-2,2721		-0,1670		2,9594		-3,4931	
DF	49,7		48,5		50.0		40,5		27,3		50,0		41,7	
Prob>[T]	0,5666		0,0922		0,6787		0,0096		0,8686		0,0047		0,0011	

Table 5. Results of Student's t-test for comparison of water variables between Community 1 and Community 2.

Variable	pH		K		Ca		Mg		Na		Cl		SO_4		EC		pHc	
Community	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
N	20	32	20	32	20	32	20	32	20	32	20	32	20	32	20	32	20	32
Mean	7,615	5,797	0,465	0,512	1,555	0,641	0,765	0,491	2,285	1,675	2,810	2,088	0,715	0,616	47,25	25,06	8,170	9,778
Std Error	0.385	0,310	0,092	0,080	0,199	0,059	0,121	0,075	0,306	0,123	0,239	0,199	0,396	0,264	5,265	1,880	0,151	0,232
Variances	Equal		Equal		Unequal		Equal		Unequal		Equal		Equal		Unequal		Unequal	
T	3,6595		-0,3799		4,4097		2,0492		1,8514		2,2916		0,2174		3,9686		-5,8145	
DF	50,0		50,0		22,3		50,0		25,2		50,0		50,0		23,9		48,6	
Prob>[T]	0,0006		0,7056		0,0002		0,0457		0,0758		0,0262		0,8288		0,0006		0,0001	

Table 6a. Results of Tukey's HSD test comparing soil variables of the top horizon between Community 1 and Community 2. Only the variables which are significantly different between the communities have been included. Means with the same letter are not significantly different.

COMMUNITY		Community 1	Sub-community 2.1	Sub-community 2.2
N		20	22	10
pH	Group	A	B	C
	Mean	4,532	3,793	3,042
Mg	Group	B	A	A
	Mean	525,1	1082,6	933,5
% Organic	Group	B	A	A
	Mean	7,083	13,625	17,215

Table 6b. Results of Tukey's HSD test comparing the soil variables of the lower horizon between Community 1 and Community 2. Only the variables which are significantly different between the communities have been included. Means with the same letter are not significantly different.

COMMUNITY		Community 1	Sub-community 2.1	Sub-community 2.2
N		20	22	10
pH	Group	A	A	B
	Mean	4,544	4,132	3,266
Mg	Group	B	B	A
	Mean	220,4	325,0	1381,3
% Organic	Group	B	B	A
	Mean	1,763	3,980	11,896

Table 7. Results of Tukey's HSD test comparing water variables between Community 1 and Community 2. Only the variables which are significantly different between the communities have been included. Means with the same letter are not significantly different.

COMMUNITY		Community 1	Sub-community 2.1	Sub-community 2.2
N		20	22	10
pH	Group	A	A	B
	Mean	7,615	6,391	4,490
Ca	Group	A	B	B
	Mean	1,555	0,709	0,490
EC	Group	A	B	B
	Mean	47,250	22,364	31,000
pHc	Group	C	B	A
	Mean	8,170	9,205	11,040

CAPTIONS FOR FIGURES

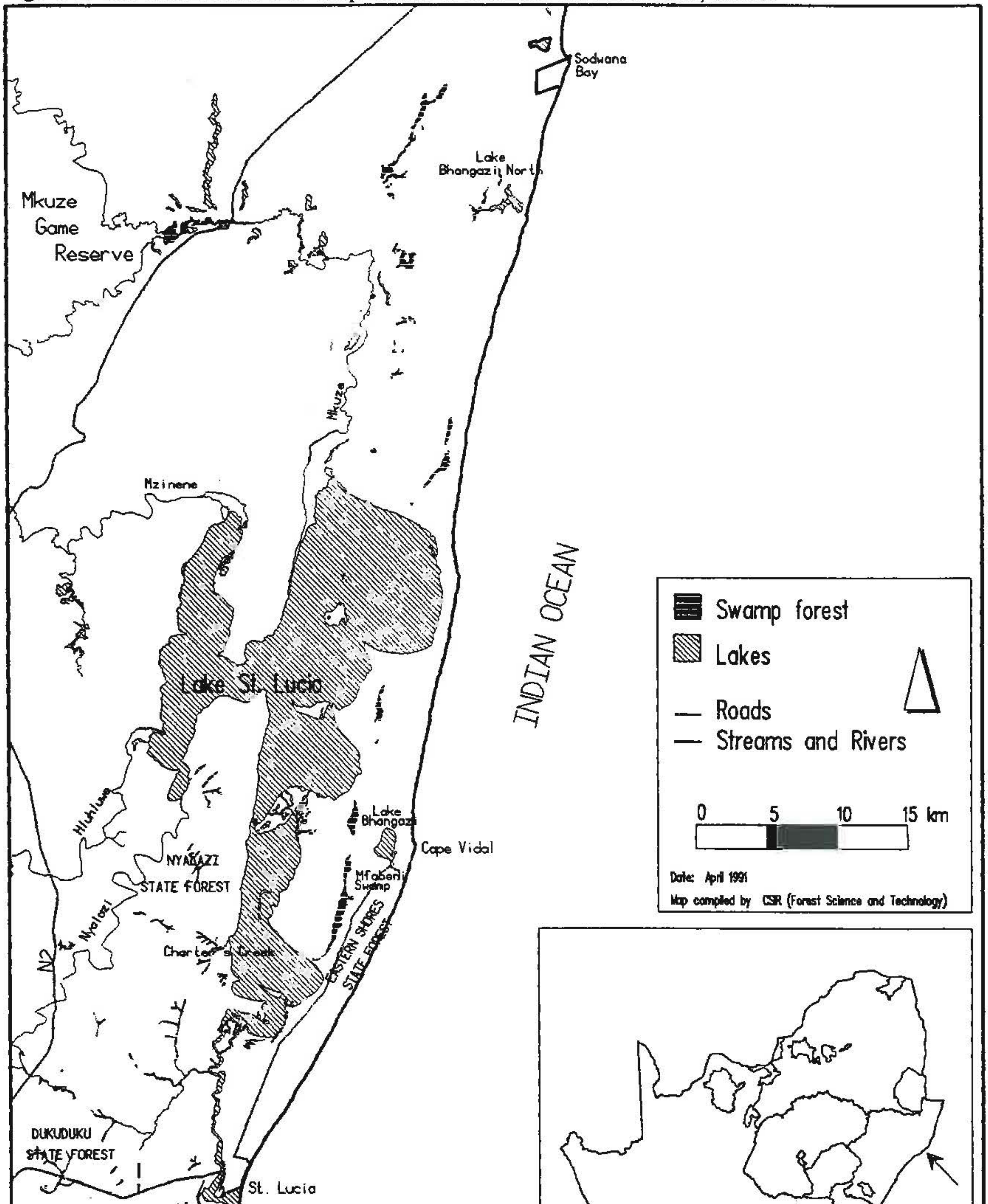
Figure 1. The distribution of swamp forests in the Lake St. Lucia area.

Figure 2. Diameter class distribution of Community 1, and sub-communities 2.1 and 2.2. Note that the scale for number of stems per hectare varies between the histograms.

Figure 3. Diameter class distribution of the ten most common tree species in the swamp forests of the Lake St. Lucia area, Natal. Note that the scale for number of stems per hectare varies between species.

Figure 4. Ordination diagrams following canonical correspondence analysis of seven soil variables and nine water variables. The samples were collected in selected swamp forests in the Lake St. Lucia area, Natal. Each plot is represented by a circle, cross or diamond, indicating to which community it belongs. Each variable is indicated by an arrow which points in the direction of maximum change of that variable. Variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and so more closely correlated to the pattern of community change shown in the diagrams. Chemical symbols have been used to label variables, except for electrical conductivity ("EC") and % organic matter ("OCarb"). In the soil variable diagram, variables relating to the top horizon are labelled with a "1", and variables relating to the lower horizon with a "2".

Figure 1. The distribution of swamp forests in the Lake St. Lucia area, Natal.



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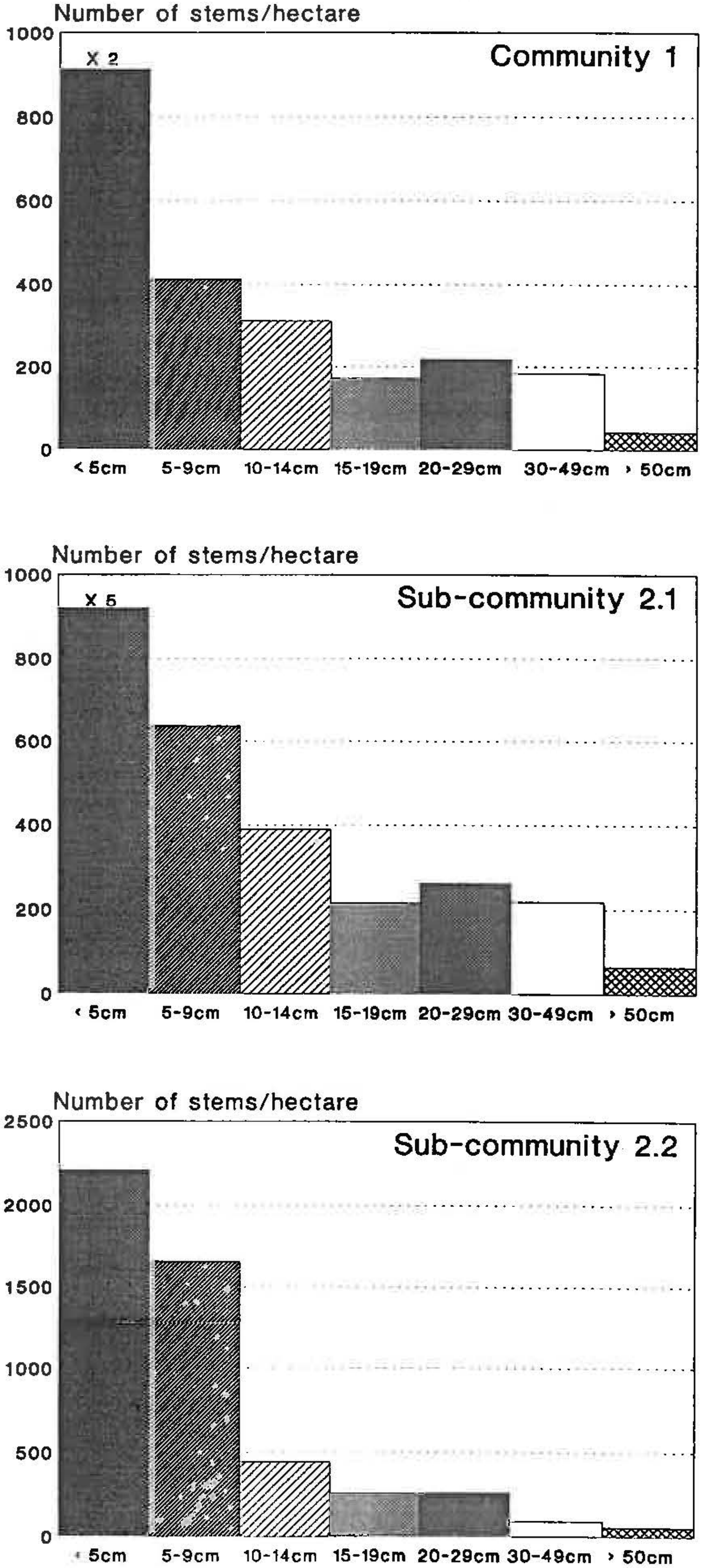

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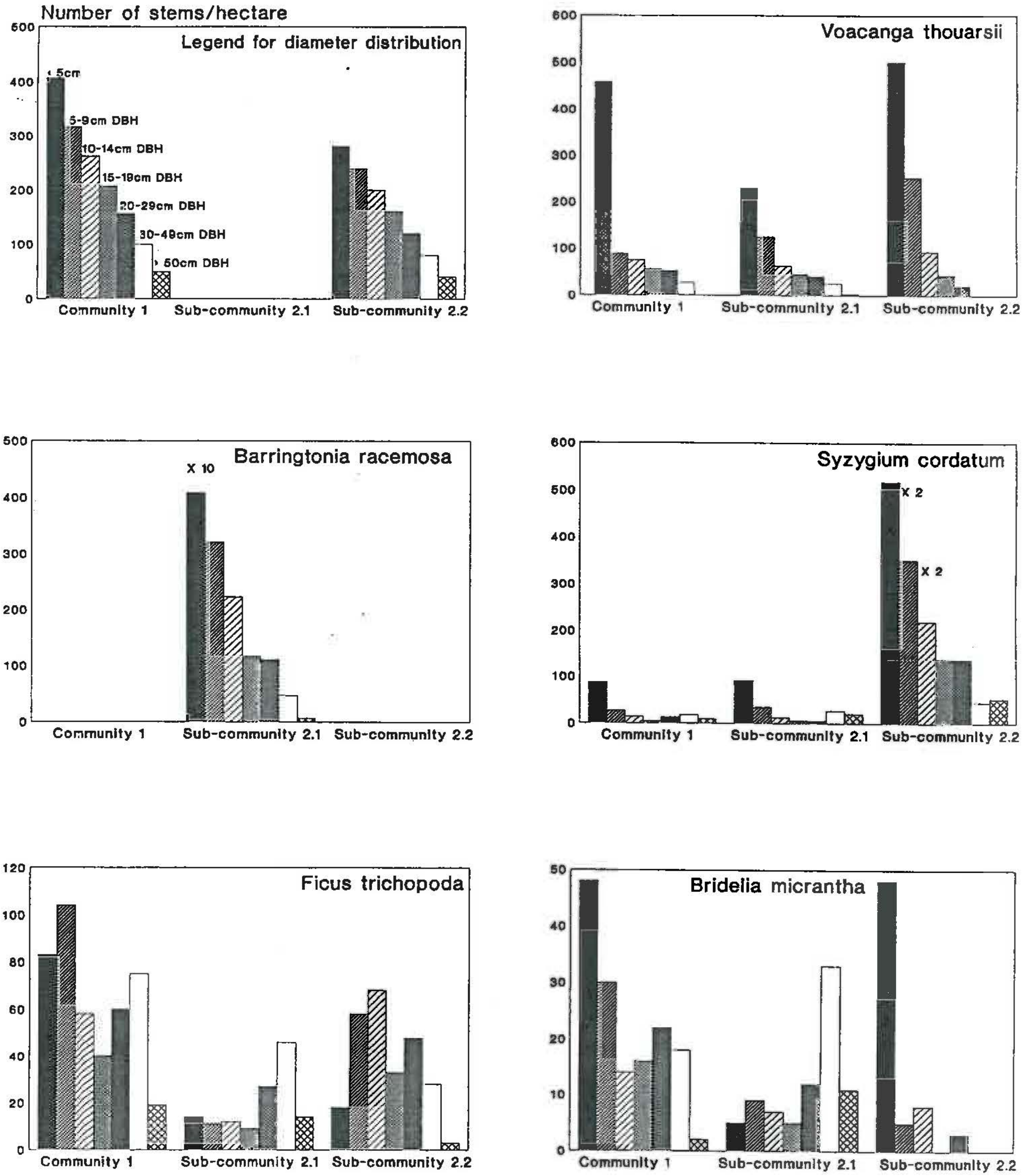

Figure 3. Continued

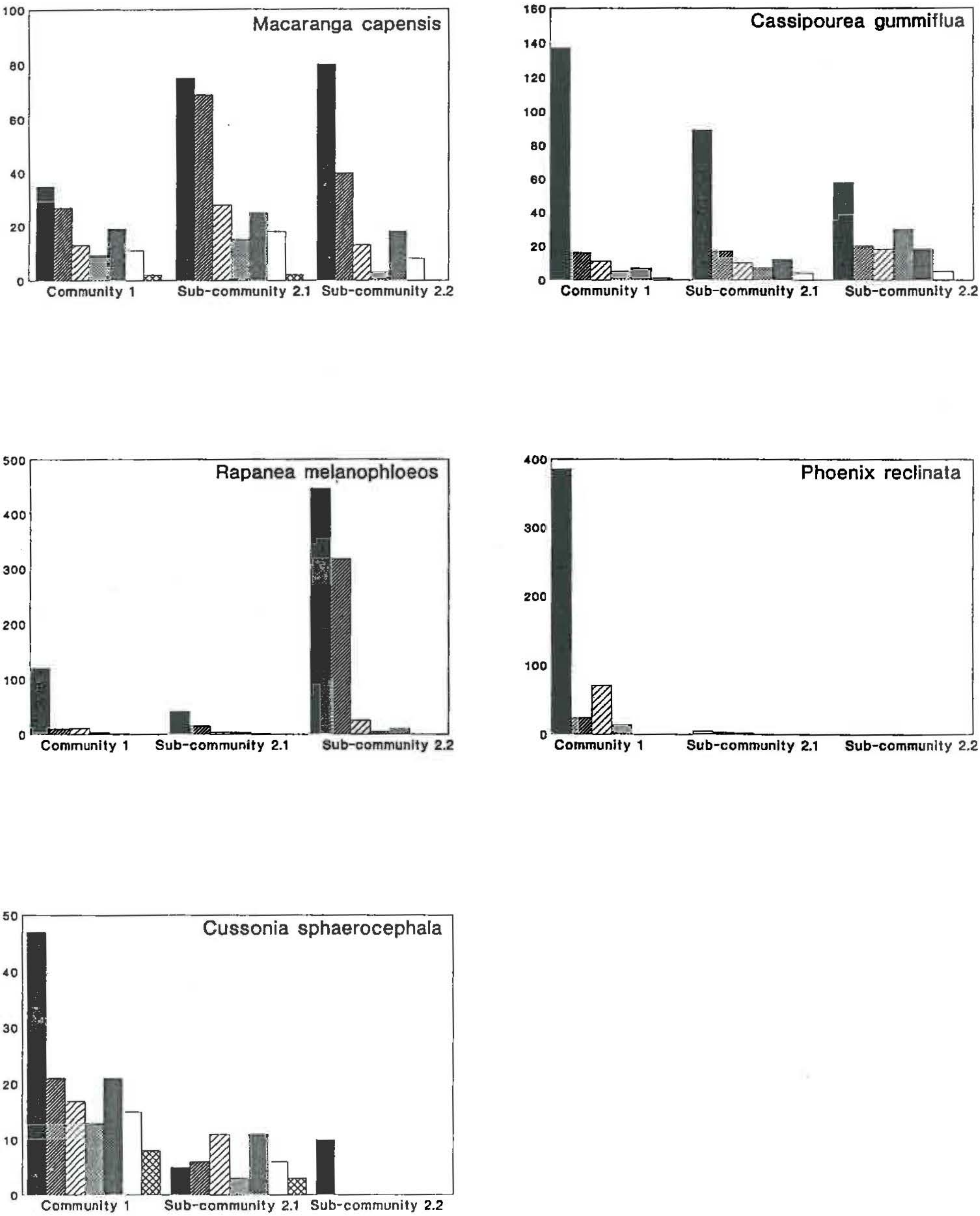

Figure 4. Ordination diagrams following canonical correspondence analysis of seven soil variables and nine water variables. The samples were collected in selected swamp forests in the Lake St. Lucia area, Natal. Each plot is represented by a circle, cross or diamond, indicating to which community it belongs. Each variable is indicated by an arrow which points in the direction of maximum change of that variable. Variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and so more closely correlated to the pattern of community change shown in the diagrams. Chemical symbols have been used to label variables, except for electrical conductivity ("EC") and % organic matter ("OCarb"). In the soil variable diagram, variables relating to the top horizon are labelled with a "1", and variables relating to the lower horizon with a "2".