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The Ecology and Species Richness of the Different Plant Communities Within Selected Wetlands on the Maputaland Coastal Plain, South Africa

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Additional information is available at the end of the chapter

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1. Introduction

The Maputaland Coastal Plain (MCP) is located on the eastern seaboard of southern Africa in KwaZulu-Natal. This area is renowned for its distinct geological history, rich biodiversity, diverse ecosystems, and internationally recognized wetlands (Figure 1). The KwaZulu-Natal Province has the second highest wetland surface area in South Africa [1], and the MCP itself contains a very rich collection of surface water bodies. This includes rivers, floodplains, estuaries, swamps, pans, and coastal lakes [2]. Land use on the MCP is mainly dominated by protected areas, agricultural practices and rural areas. There are currently few urbanized areas. Despite this few wetlands are still intact. Although wetlands play an important role for especially the local inhabitants on the MCP, its value is still underestimated, and little has been done for the promotion of conservation and sustainable utilization of these sensitive ecosystems.

Even though the vegetation of the MCP is remarkably diverse, few vegetation studies have been done on wetlands in the area. The major vegetation types of the MCP have been broadly described by Moll [3,4], and Morgenthal [5]. Tinley [6, 7, 8] conducted vegetation surveys along the coast, while Lubbe [9] conducted a detailed vegetation study of the coastal strip. Many detailed local vegetation studies have been conducted in the protected areas on the MCP but very little in the unprotected areas of the MCP. None of the studies mentioned above provide detailed descriptions of the wetland vegetation and their species richness. The only vegetation study focusing exclusively on wetlands is on the Mfabeni mire in the iSimangaliso Wetland Park [10].

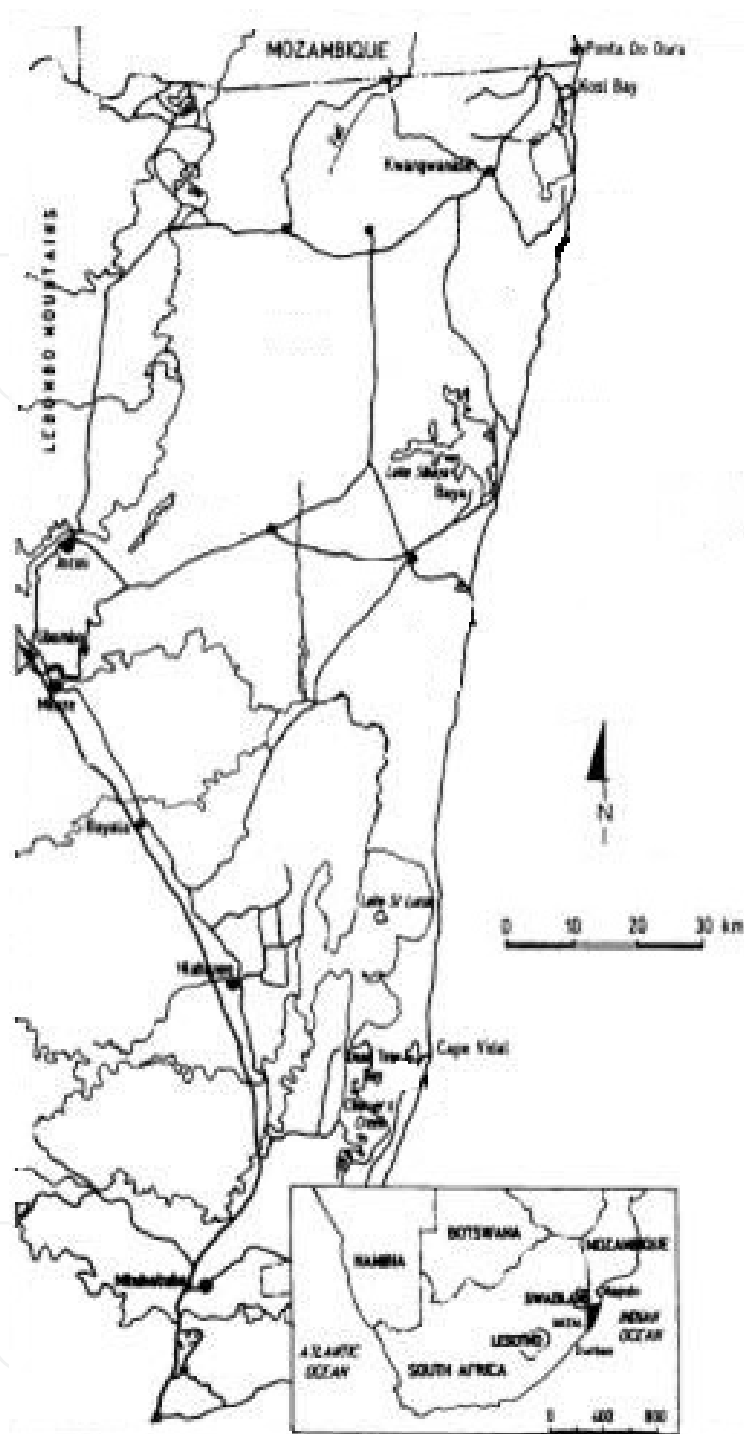


Figure 1. Locality of Maputaland within the South African context

Furthermore, the delineation of wetlands on the aeolian derived sandy soils associated with the MCP is regarded as problematic when using the soil form and-wetness indicators described by the Department of Water Affairs and Forestry (DWAf 2005) [11]. However, the distinct changes in plant species composition along the wetness gradient of a wetland provide an indication of wetland zoning [12, 11] and therefore guides the delineation procedure.

This study aims to elucidate the relationship between vegetation communities, plant species richness, and their environmental setting within the various wetland types on the MCP, in order to contribute to the understanding of wetland zones.

2. Study area

The MCP is demarcated by the Mozambican border in the north; the town Mtunzini in the south; the Indian Ocean in the east; the Lebombo Mountains in the north-west; and the N2 on the south-west. This study focuses on the northern parts of the MCP only (Figure 1).

The MCP has a subtropical climate with very hot summers and mild winters. The area receives 60% of its rainfall during summer and 40% during winter, with a mean annual precipitation of 963 mm [13]. Rainfall decreases sharply from east to west, with an approximate mean of 1200 mm at the coast, and 800 mm – 1000 mm at the crest of the Lebombo Mountains [13].

Aeolian distributed sands from the Tertiary and Quaternary period dominate most parts of the MCP. These sands are relatively infertile and of low-productivity [14]. The study area is characterized by undulating dune topography located up to roughly 70 m above sea-level [15]. In the east the Plain is separated from the Indian Ocean by an uninterrupted barrier dune system [14]. A long, relatively flat coastal plain stretches between the Lebombo Mountain Range and the coastal barrier dunes. Dune cordons occurring sporadically all over the MCP are interspersed with various wetland types such as floodplains, lakes, fens, swamp forests and pans [16]. Groundwater is the principal source of water for most of the lakes and wetlands in Maputaland [17], and moves rapidly through the system due to high permeability, high rainfall, and low water gradients. Two primary porosity aquifers are present on the MCP—a shallow, unconfined aquifer and a deeper, confined aquifer [18]. The shallow, unconfined aquifer is driven by rainfall which infiltrates and percolates through the sandy soil until it reaches the impermeable Kosi-Bay Formation, where after the water then moves laterally to exit the aquifer in the form of a surface water source.

In terms of biodiversity the MCP fall within the Maputaland Centre of Endemism Centre. This is one of Africa's most important biodiversity and endemism hotspots, and is located at the southern end of the African tropic where many plant and animal species reach the limit of their range. An assortment of diverse ecosystems and many broad ecological zones such as thicket, grassland, bushveld, forest, sand forest and swamp forest occur here [19].

Most of the wetlands occurring outside conservation areas are degraded. Local inhabitants of the area utilise the wetland areas extensively for subsistence agriculture due to the infertile nature of the sandy soil. A recent threat to the health of wetlands is the informal plantations that have sprung up all over the MCP during the past 20 years. These *Eucalyptus* plantations have a marked effect on the water table and the subsequent dynamics of the wetlands systems in the area. The MCP is rich in peatlands and contains about 60% of the estimated peat resources of South Africa [20]. This region contains the largest and highest density of peatlands of all the Peat Eco-Regions. It is estimated that 60 – 80% of these peatlands are currently being utilised by the local community for subsistence agriculture and other uses [21].

Five wetland types were identified and investigated in this study (Figure 2):

- Interdune-depression (IDD) System –
 - Scattered depression type wetlands between vegetated coastal dunes,
 - Linked with the regional water table,
 - Peaty soil in the pristine wetlands [33],
 - Intense local utilisation of the fertile peaty soils for subsistence.
- Muzi North Swamp System (MS) –
 - A linear valley-bottom system,
 - Linked with the regional water table,
 - The permanently wet areas of the system are peaty,
 - Clay lenses occur at 300 – 500 mm depth on the banks of the system,
- Perched Pan (PP) and Depression (DP) Systems –
 - A series of scattered seasonal pans occurring parallel to the MS system,
 - Inside the Tembe Elephant Park the pans occur as open areas surrounded by closed woodland (PP System),
 - Outside the Park the pans are open and degraded (DP System),
 - High clay content in the soil results in a perched water table for several months per year [31],
 - The pans are clay-rich, calcareous duplex soils.
- Upland Wetland (PL) System –
 - Located on the upland flat area between the Tembe Elephant Park and Manguzi,
 - Slightly undulating Lala Palm veld with interspersed spaces of open, moist grassland,
 - Depressions occur in large patches in the Palm Veld.
 - These wetlands are seasonal and water table fluctuation plays a prominent role [17].

3. Methods

Wetland areas occurring between the Tembe Elephant Park (TEP) and Kosi-Bay were identified using Google Earth and 1:3000 Orthophotos, and verified with a field visit to the area. The wetlands were selected based on accessibility, safety, land owner consent, data availability, and land use.

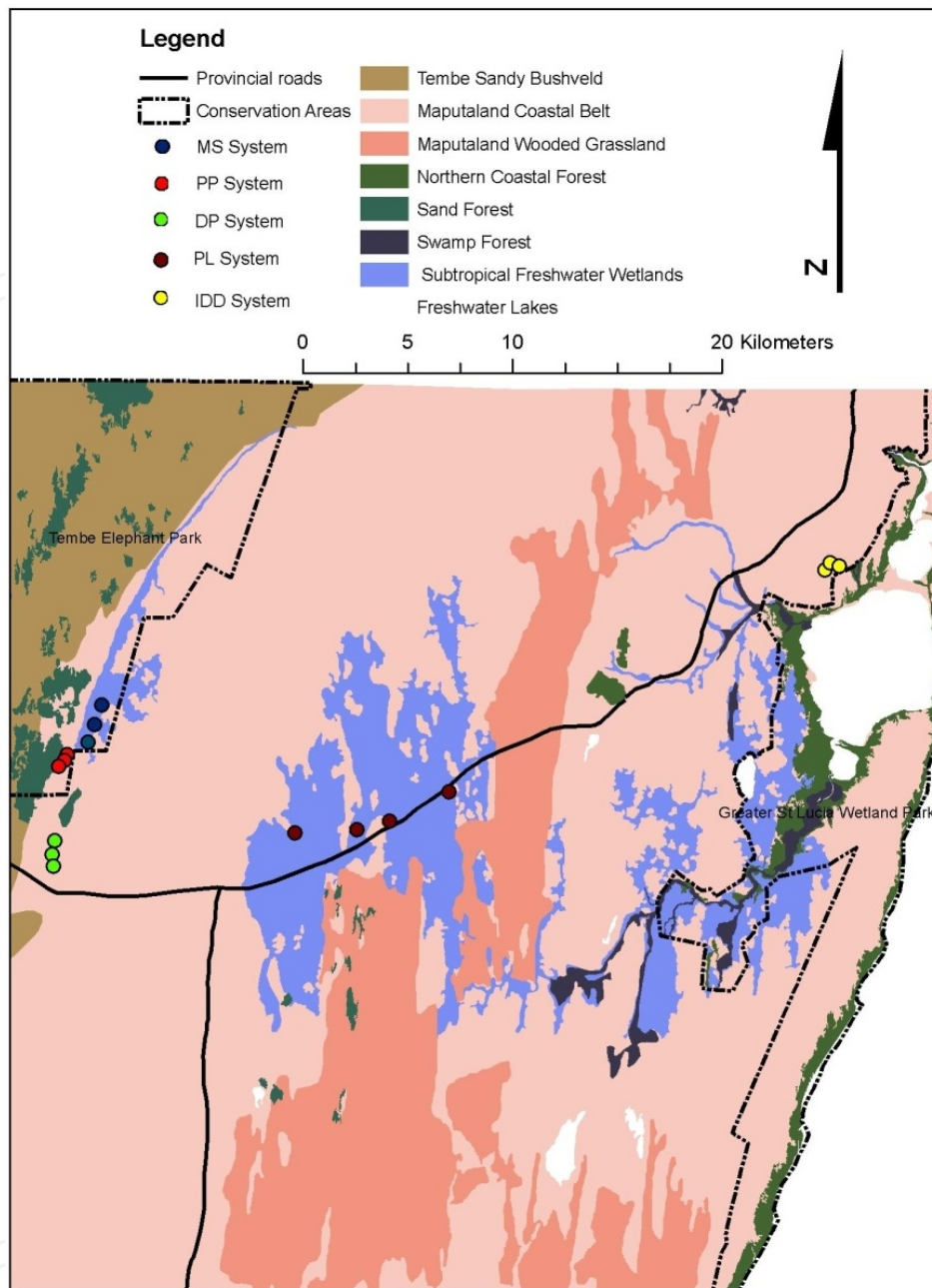


Figure 2. Wetland systems occurring in the northern parts of the Maputaland Coastal Plain.

Between three to five wetlands in each system were selected to be surveyed. These wetlands were first stratified into their various vegetation zones. Between three and five vegetation zones were identified in each wetland. For the purpose of the data collection in the field the different zones sampled were based on vegetation communities observed and not on hydrological regime. Therefore these zones were not termed 'permanent', 'seasonal', 'temporary', or 'terrestrial', but rather as Zone 1, Zone 2, Zone 3, etc (Figures 3 and 4). However after the data analysis the different zones were grouped into the different wetness zones as listed above and discussed accordingly under the discussion section.

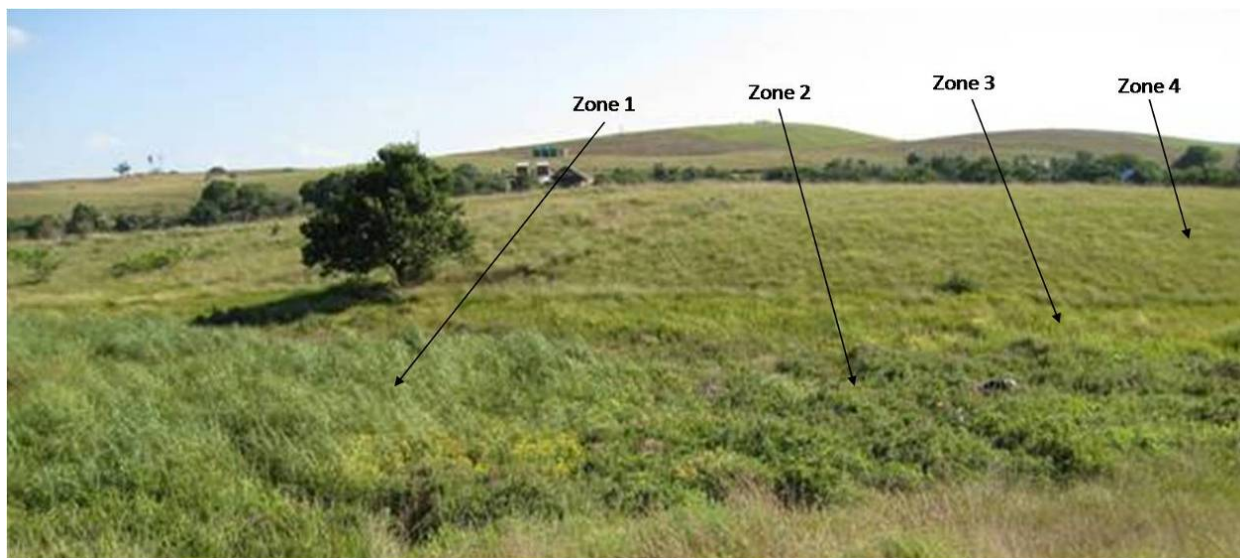


Figure 3. The Interdune-depression (IDD) System with an example of the zone delineation.

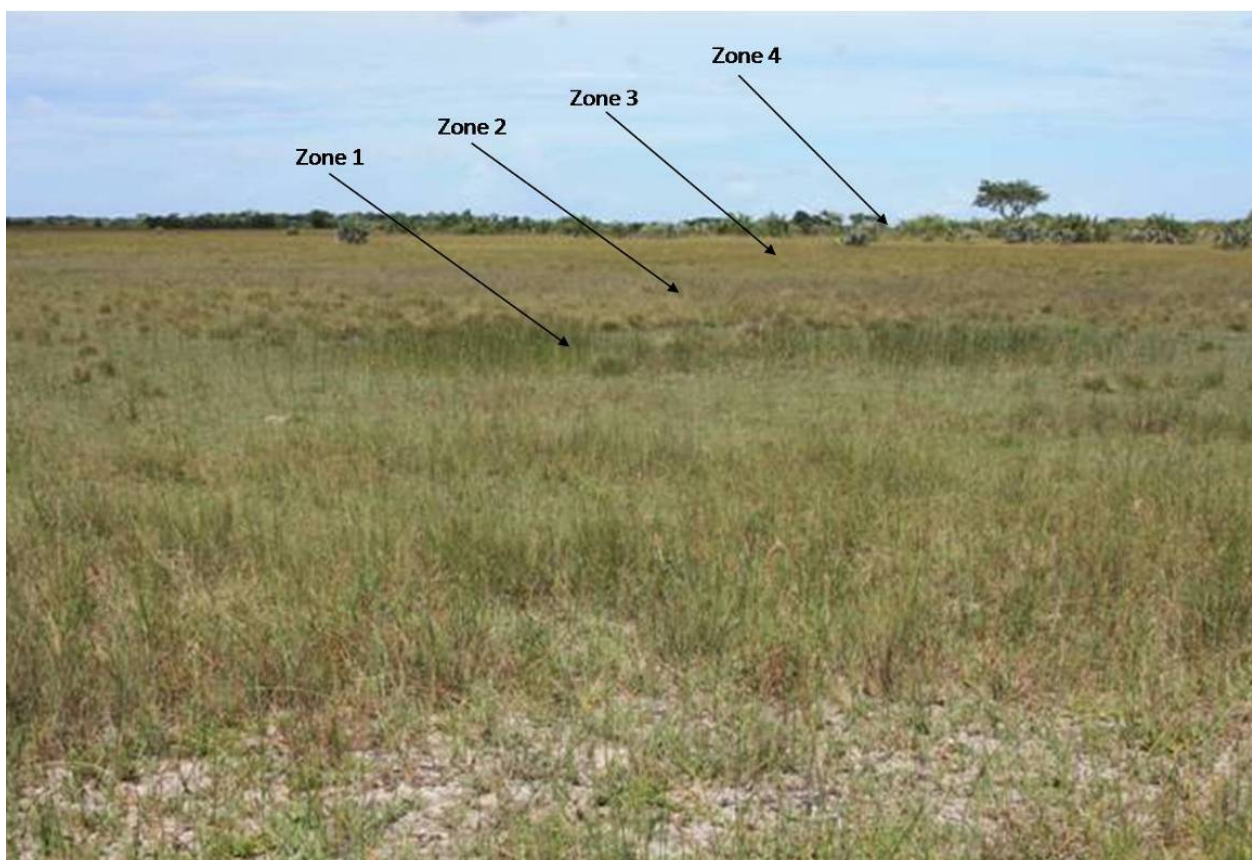


Figure 4. The Upland Wetland (PL) System, with an example of zone delineation.

Vegetation surveys were conducted in March 2010 following the Zurich-Montpellier (Braun-Blanquet) School of total floristic compositions approach [22]. A total of 72 sample plots (2 m

x 2 m) were placed within the different zones in a stratified random manner. Plant species were identified in the field, while the unknown plant species were collected and sent to the South African National Biodiversity Institute for identification.

The vegetation relevés were captured into TURBOVEG for Windows 1.97 [23] and exported to JUICE 6.5 [24]. A modified TWINSpan was performed in JUICE using the Whittaker's beta-diversity, with the following pseudospecies cut-levels: 0, 1, 5, 25, 50, and 75. The Fisher Exact Fidelity Test at $P < 0.001$ were used. The final classification was manually refined according to the Braun-Blanquet procedure [25]. No re-arrangements of clusters or relevés were done, but only species groups were manually re-arranged.

Six different ordination methods were applied to the plant community data in PCOrd [26]-the Bray-Curtis ordination, Canonical Correspondence Analysis, Weighted Averaging, Reciprocal Averaging, Detrended Correspondence Analysis (DCA), and Nonmetric Multidimensional Scaling (NMS). The DCA and NMS analyses gave the best results. The DCA ordination results are presented in this study, as it emphasized the variation and combination of the plant communities better than the NMS results. Various environmental factors thought to influence the distribution of the vegetation communities were superimposed on the ordination results. The overlay of the floristic communities identified by [27], the five wetland systems, and substrate type are included in the final results.

The Chi-Square Test [28] was performed on the data to determine whether significant differences exist between the species richness of the different plant communities.

4. Results

The modified TWINSpan analysis [29] resulted in the identification of 11 plant communities that can be grouped into eight major communities and six sub communities. The results of the DCA ordination for all the plant communities are contained in Figure 5. From the DCA ordination axes 1 and 2 were selected as it was the most interpretable ordination. An Eigenvalue of 0.933 and 0.828 were obtained for Axis 1 and Axis 2 respectively.

The clay communities (communities 1 – 3) are positioned distinctly to the right of the ordination diagram. The communities which are located on predominantly sandy substrates (e.g. Community 4) are found on the extreme opposite end from the clay communities. The close proximity between Community 2 and sub community 6.2 is because both originate from the PP system. Sub communities 7.1, 7.2, and 7.3, all from the MS system, are affiliated with each other despite hydrological differences between the different zones. Sub community 5.1 and most of Community 8 originate from the PL System, explaining this association. The significant distance between sub community 5.1 (PL System) and 5.2 (IDD System) is as a result of the fact that they occur in different systems, despite similar environmental settings. Sub community 7.3 has a wide distribution, as some of its dominant species occur in other communities as well. Of these the graminoids *Stenotaphrum secundatum* and *Cynodon dactylon* are known to be variable in their habitat preference, and are not limited to a certain environment.

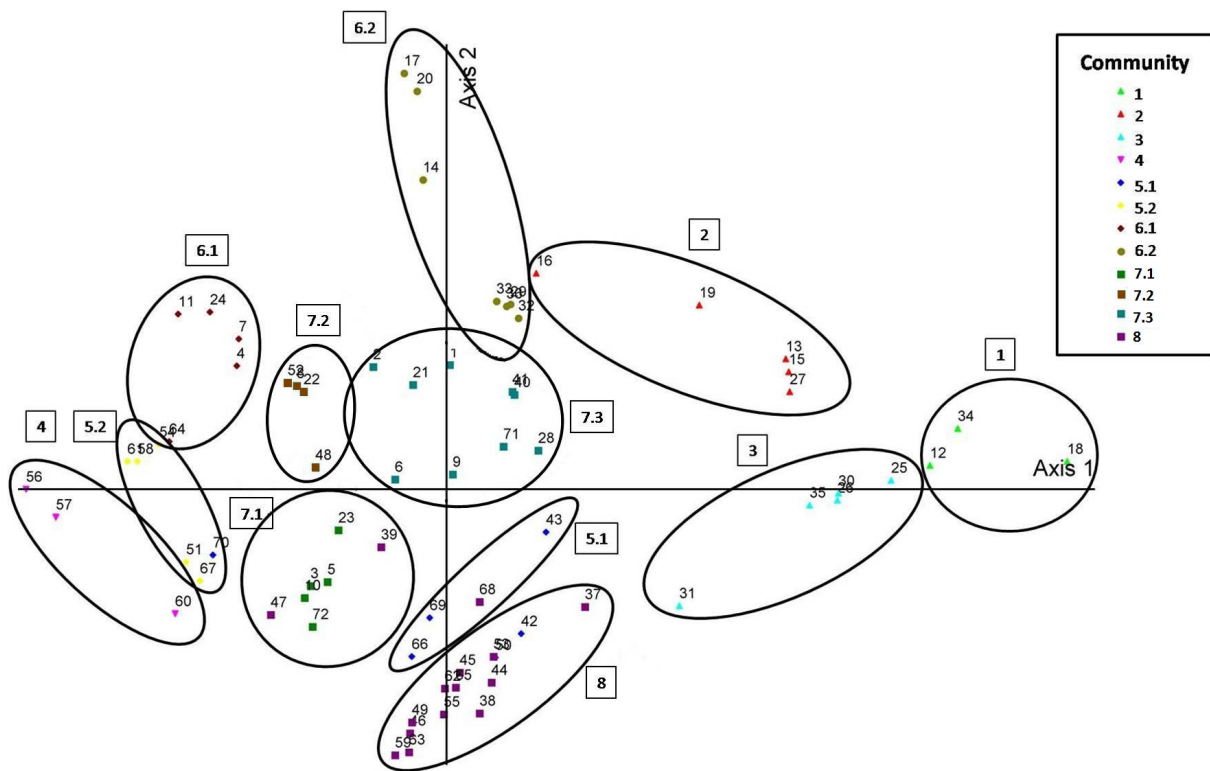


Figure 5. DCA ordination indicating clustering of communities.

4.1. Substrate overlay

Substrate has a strong influence on the spatial occurrence of vegetation communities and plant species. The clay communities (Communities 1 – 3 and 6.2) cluster strongly together with the communities occurring on duplex soil (sub communities 6.1 and some of 7.1) to a lesser degree so (Figure 6). A part of sub community 7.1 is found near the sand and high organic clusters because they are not only characterized by duplex soils, but also by higher organic matter content. The relationship between the plant species assemblages occurring on sandy and the high organic substrates are interesting, as the “High Organic” and the “Sand” communities form two overlapping clusters with a wide distribution. The “High Organic” cluster originates from Community 7 and is regarded as the “Organic MS System”. This cluster is seasonally to permanently flooded, but because it originates from the MS System (which is characterized by clay lenses on the banks of the wetland) it occurs close to the cluster with the duplex substrates. Towards the bottom of Axis 2 the “Sand & High Organic” cluster contains Community 8 (seasonally and permanently flooded) (Figure 4) which originates from the sandy PL and IDD Systems.

4.2. Wetland system overlay

It was hypothesized that due to the divergent characteristics and environmental settings, the five wetland systems would contain plant communities entirely unique to each system. However, the dominant division was mainly between the two clay systems (PP and DP) and

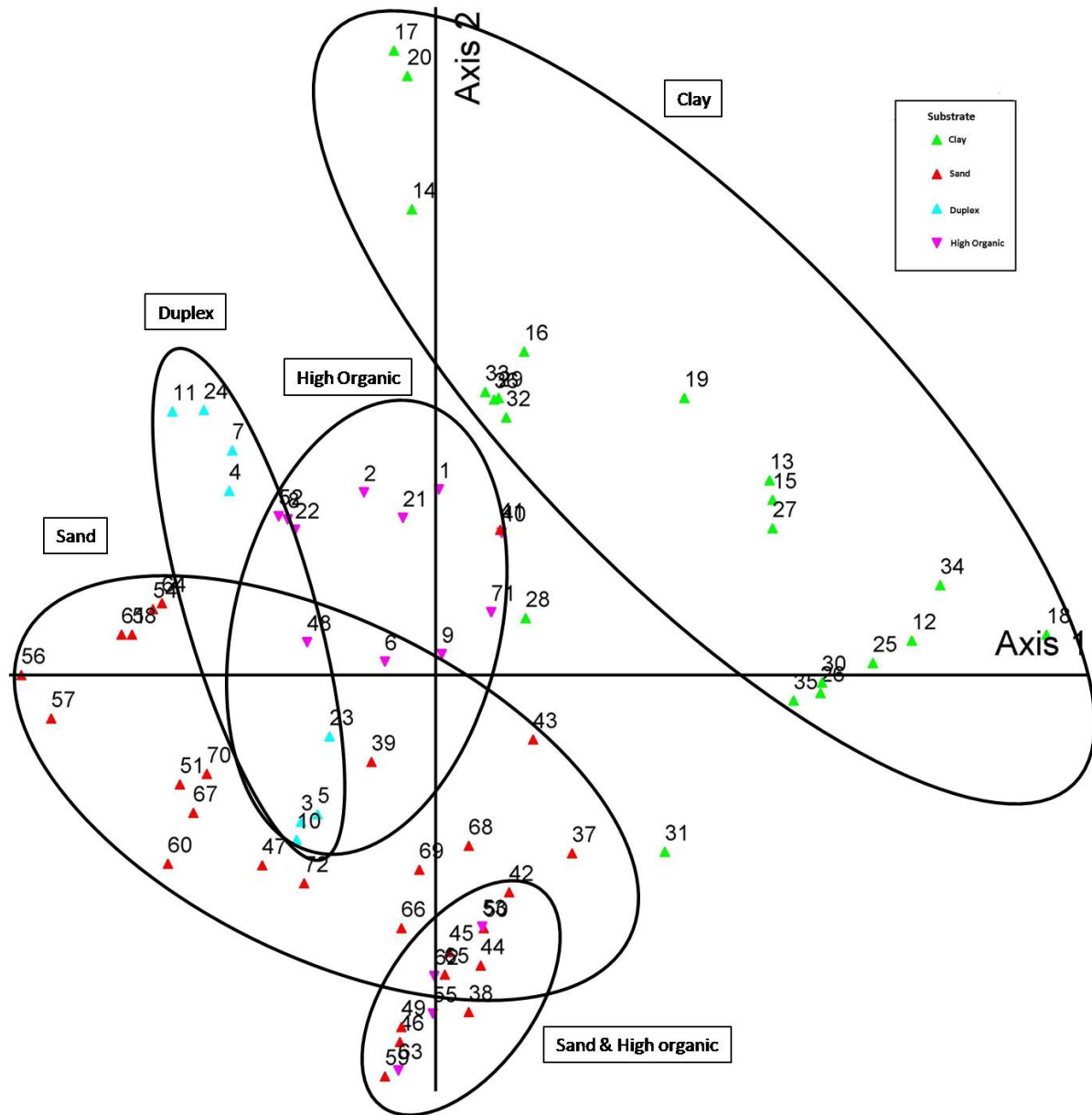


Figure 6. DCA ordination with substrate overlay.

the rest of the systems (MS, IDD & PL) (Figure 7), which obscured all other environmental distinctions between plant communities. Other differences in terms of vegetation composition could be ascribed to system characteristics such as substrate, geology, and hydrological regime. There exists no differentiation between the PL and IDD system, which is unexpected as these two systems are so distinct from each other.

In order to elucidate the relationship between the MS, IDD & PL systems, the clay PP and DP Communities (Communities 1-3 and 6.2) were eliminated, and the data analysed again. The communities on high organic substrates with a seasonally to permanently wet hydrological

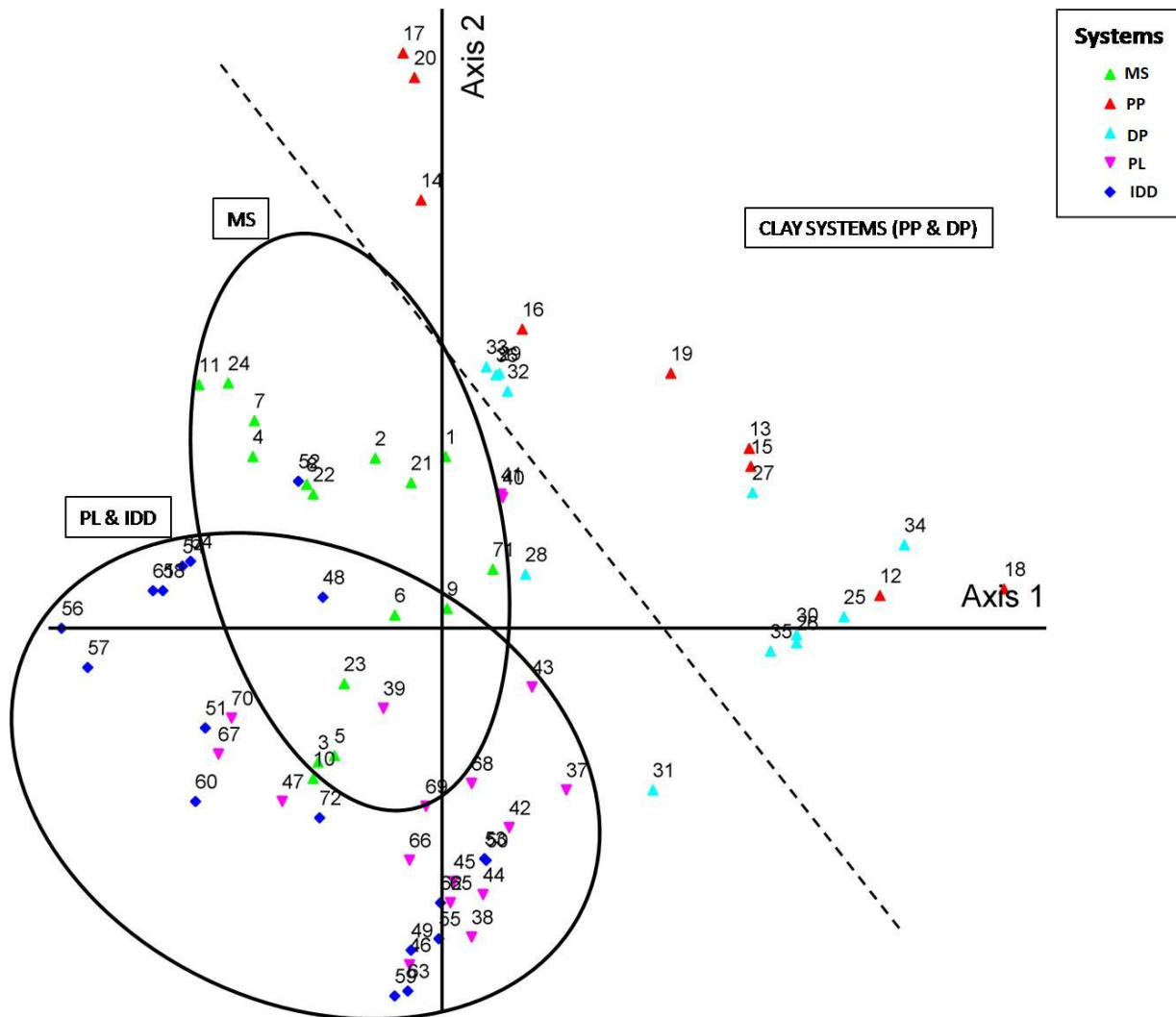


Figure 7. DCA ordination with Systems overlay.

regime (Communities 7 and 8) cluster to the left, while the communities on seasonal duplex soils and more terrestrial sandy soils (Communities 4 – 6.1) cluster to the right (Figure 8). In addition to the influence of the type of substrate on plant assemblages, there is therefore also a strong dry to wet influence.

4.3. Species richness

The species richness and average species per 4m² of each community is indicated in Table 1. The average species richness per 4m² is clearly lower in Communities 1 – 4 (the seasonal zone of the clay wetlands) than in the rest of the communities. There was a significant association between the number of plant species and plant communities present at $X^2(7)=382.35$, $p < 0.0001$. Sub communities 5.2 and 6.1 have exceptionally high species richness. The only environmental characteristic that these two sub communities have in common is that both communities are

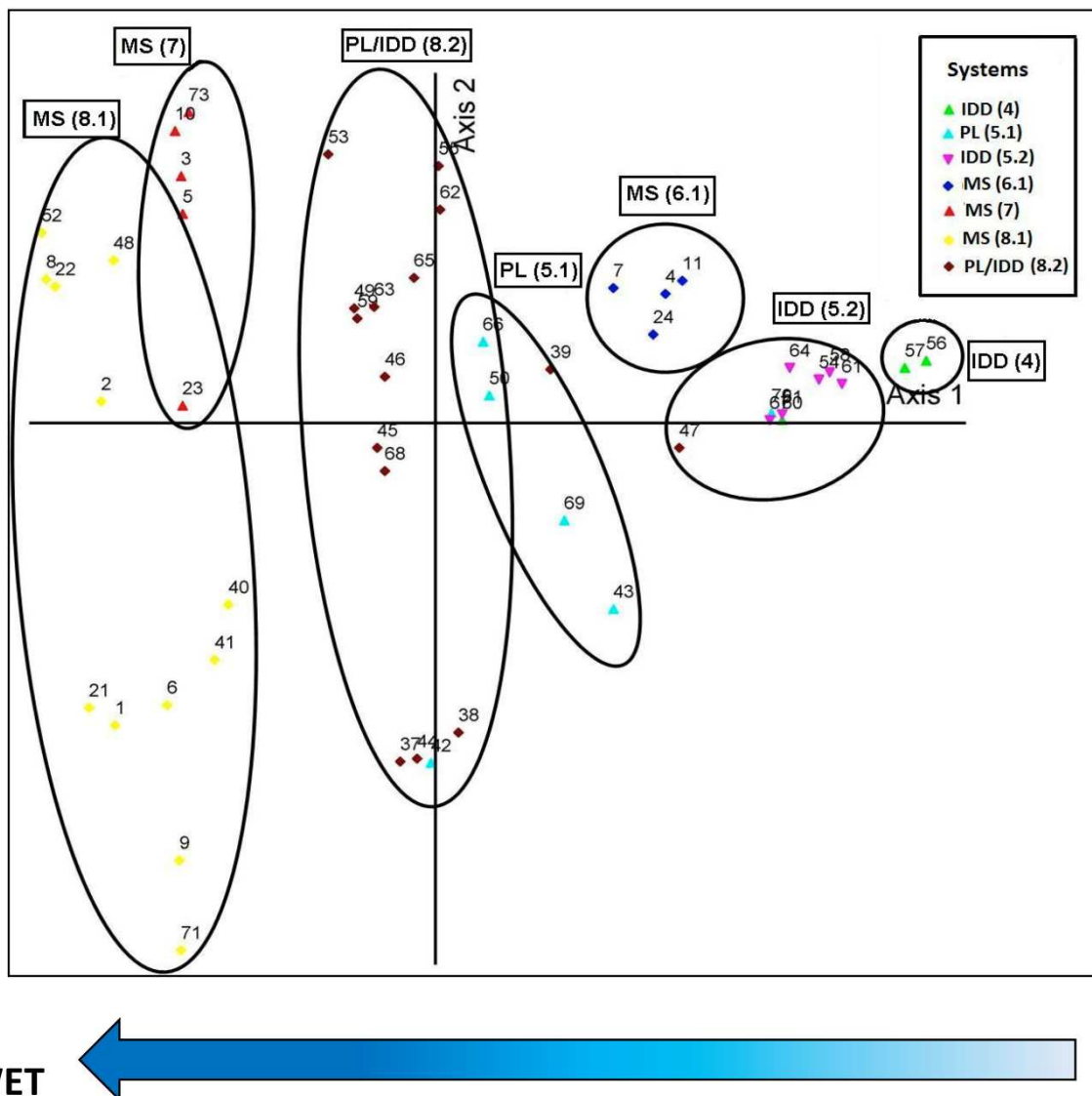


Figure 8. DCA ordination with community overlay of only the MS, PL, and IDD Systems which indicates a gradient from terrestrial to seasonally and permanently wet communities.

located well outside the wetland in the terrestrial zone. Based on the standardized residuals, species in Communities 1 to 4 are underrepresented (less than -1.96) and those in communities 5 to 8 are over represented (greater than 1.96).

The average species richness for the various systems is contained in Table 2. As in Table 1 it is clear that the clay PP and DP communities are more species poor than the rest of the wetland systems. The highly organic IDD system is significantly more species rich. Although the MS system also has high organic substrate, it contains many clay-related plant assemblages due to the clay lenses on the edges of the peat substrate.

The plant assemblages give a good indication of the wetness levels of the various zones. Additionally the peatlands on the MCP are permanently wet, and all connected to the groundwater table [17]. This was used to assign the various plant communities to the three

wetness zones indicated in Table 3. Usually species richness decrease with increasing wetness levels as few plant species are adapted to waterlogged soil [12]. However, in this study species richness in the permanently wet (therefore high organic and peat substrate) zones is actually much higher than that of seasonally wet zones.

Community	Species richness	Average species per 4m ²	Lower	Higher
1	9	3	2	4
2	32	6.4	4	10
3	22	4.4	3	7
4	19	6.33	5	7
5.1	58	9.7	5	13
5.2	103	17.17	14	24
6.1	59	14.75	12	19
6.2	75	10.7	8	17
7.1	33	6.6	4	10
7.2	26	6.5	2	10
7.3	79	8.78	4	14
8.1	70	11.7	6	17
8.2	67	7.44	4	10

Table 1. Species richness of each community.

System	Community	Average species per 4 m ²
PP & DP	1; 2; 3; 6.2	6.1
MS	6.1; 7.1; 7.2; 7.3	9.2
IDD	8.1; 4; 5.2	11.7
PL	5.1; 8.2	8.6

Table 2. The average species richness for the various systems.

Zone	Community	Average species per 4 m ²
Permanently wet	8.1; 7.3; 7.2	8.993
Seasonally wet	8.2; 7.1; 4; 1; 2; 3	5.695
Terrestrial	6.2; 6.1; 5.1; 5.2	13.08

Table 3. The average species richness for the various wetness levels.

5. Discussion

5.1. Muzi Swamp (MS) system

Characteristic plant species of the Muzi Swamp System

Terrestrial zone:*Acacia nilotica* & *Hyperthelia dissoluta*

Seasonal zone:*Imperata cylindrica*

Permanently wet zone:*Cladium mariscus*, *Phragmites australis*, *Stenotaphrum secundatum*, *Cynodon dactylon*, *Dactyloctenium aegyptium*

Typical plant communities: 6.1, 7.1, 7.2, 7.3

There is a distinct division between the terrestrial zones (sub community 6.1) and the permanently and seasonally wet zones of the MS System (Community 7). The grass *Imperata cylindrica* invariably characterizes the seasonal zone (sub community 7.1); even though this zone is very closely associated with the permanently wet zones (sub community 7.2 and 7.3). This community is described in Matthews *et al.* [31]. It also correlates with the “proximal-seasonally inundated floodplain” in Patrick & Ellery [30], in that it is functionally connected to the channel by being exposed to seasonal flood events and sedimentation.

The MS system is characterized by both a peat substrate which has a relatively high species richness as well as clay lenses on its edges which, in this study, has shown to have a lower species richness.

5.2. Perched Pans (PP) and Depressions (DP) clay systems

Characteristic plant species of the PP and DP (clay) systems (Figure 9)

Terrestrial zone:*Acacia nilotica*, *Acacia karroo*, *Justicia flava*, *Panicum maximum*

Seasonal zone:*Cyperus fastigiatus* (PP System) & *Echinochloa colona* (DP System)

Permanently wet zone:*Lemna gibba*

Typical plant communities: 1, 2, 3, 6.2

Matthews [30] describe two communities which occur on clay pans in the TEP-a “grassland on clay between thicket and pan marsh edges” Community, which does not correlate with what was found in the PP System; and a “*Nymphaea nouchali* aquatic vegetation in marshes and pans” which do correlate with the inundated zones found in the PP and DP Systems. There is a strong division between zone 1 (Community 1) and zone 2 (Community 2) of the PP System; as well as zone 1 (Community 1) and the seasonal zone 2 (Community 3) of the DP System. Community 3 is composed of many species that are regarded obligate hydrophytes such as *Marsilea sp.*, *Pistia stratiotes*, and *Nymphaea nouchali*, yet it is regarded a seasonal zone. This classification of this community is as a result of the prominence of *Echinochloa colona* which didn't occur in open water, but in the area which is still waterlogged and able to host hydrophytic species such as those named above. *Echinochloa colona* is indicative of overgrazing and

trampling [32], and occur in wetlands due to human influences. The PP System is utilized by animals of the Tembe Elephant Park as a water hole. The trampling of the pans by large animals decreases the open water zone and compacts the seasonal zone, destructing the habitat of the hydrophytes that could have occurred there.

The terrestrial zones cluster together into one community (Community 6), despite the differences that divide the inundated zones of the DP and PP System. Community 6 is far removed from Communities 1-3 (the wet and seasonal zones of the PP and DP Systems). The association of sub community 6.1 (MS System) with 6.2 (PP System) is based on the similarity of the substrate – a sandy topsoil underlain by a horizon with a significant increase in clay (duplex soil).

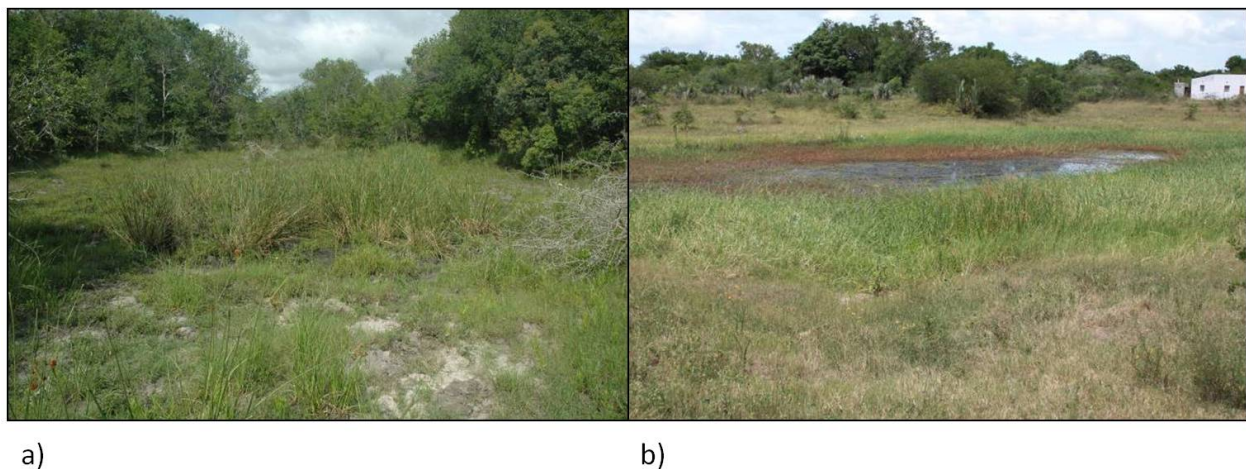


Figure 9. The floristic differences between the two clay systems with a) PP System and the b) DP System.

The species richness in Community 1 (the inundated community of both the PP and DP systems) is much lower than in Community 2 and 3 (the seasonal zones) and sub community 6.2 (the terrestrial zones). These results highlight the difference between species richness in high organic, fertile substrate versus the poor species richness on clay substrates, and supports the general rule of decreasing species richness with increasing wetness. As with the other systems the species richness is higher in the terrestrial zones, although still somewhat less in these clay systems as opposed to the other systems' terrestrial zones.

5.3. Interdune-depression (IDD) system

Characteristic plant species of the IDD system

The terrestrial zones of the IDD System have exclusive species assemblages. The disturbed community (Community 4) and the permanent-and seasonal zones, share many species with the PL System.

Terrestrial zone: *Themeda triandra*, *Trachypogon spicatus*

Permanently wet & seasonal zone:*Cladium mariscus*, *Cyperus natalensis*, *Hemarthria altissima*, *Thelypteris interrupta*

Disturbed seasonal zone:*Scleria sobolifer*, *Xyris capensis*

Typical plant communities: 8.1, 4, 5.2

The species composition of Community 4 illustrates the over-exploitation of the IDD system for the fertile, high organic substrate in the waterlogged areas. The permanently wet and seasonal zones are drained by trenches and drains through the wetland. The drainage lines stay visible, coining the term “fossil gardens” [33] (Figure 9 b). Only the seasonal zones from the disturbed wetlands form part of the disturbed Community 4. The permanently wet zone 1 doesn't floristically show disturbance as much as the seasonal zone, and seems to be buffered to some extent. A disturbance regime therefore has a much larger effect on the seasonal zones where the hydrological regime is variable.

The IDD and the PL Systems are generally grouped very closely together. The wet zones of both these systems occur close together in the ordination space, despite the IDD System having a permanently wet peat substrate and the PL System being periodically flooded open sandy plains. The only explanation that can be put forward for the similarity in species is that the peat might be shallow enough that the plants in the IDD System is rooted in the underlying sand substrate beneath the peat, and not necessarily in the peat itself. There is also a high similarity between the terrestrial zones of the PL (sub community 5.1) and IDD (sub community 5.2) systems, probably due to the sandy substrate of these terrestrial zones.

In the ordination results, however, these sub communities are far removed from each other. The zone differentiation in the IDD System is somewhat different to that of the other systems, as there is only a permanently wet zone and a terrestrial zone. Zones 1 and 2 cluster together in the highly organic, waterlogged community, and Zones 3 and 4 clusters together in the sandy grassland terrestrial community. This is because the transition between the permanently wet zone and the terrestrial zones is so sharp due to the steep slope of the depression, that the “seasonally wet zone” is just a small area at the slope foot. This zone is still high in organic carbon content, and therefore shares many species with the permanently wet zone.

The IDD system has the highest species richness of all the systems. This can be attributed to the high organic substrate that dominates this system. It is also devoid of clay, which seems to support a lower species diversity.

5.4. Upland Wetland (PL) System

Characteristic plant species of the PL system

Terrestrial zone:*Cyperus natalensis*, *Bulbostylis contexta*

“Wet” and seasonal zone:*Cyperus natalensis*, *Centella asiatica*, *Hemarthria altissima*, *Eragrostis heteromera*

Typical plant communities: 5.1, 8.2

Moist grasslands feature strongly in all vegetation studies done on the MCP, and are termed “hygrophilous grasslands”. Various studies [9, 34, 35, 36] detail ‘high water-table grassland’ communities termed ‘hygrophilous grasslands’, which corresponds loosely to both The PL and IDD systems. All the above studies noted dominant occurrence of *Ischaemum fasciculatum*, which was not found abundantly in the PL System. The water table of the PL System (> 3 m deep) is in most areas not as high as the hygrophilous grassland communities described by the above authors. The absence of *I. fasciculatum* from the PL System might thus be a result of the variable hydrological regime. This argument is supported by Matthews [33] who states that *I. fasciculatum* is a species which reflects periods of inundation.

There is therefore a large overlap between the terrestrial zones and the wetter zones of the PL and IDD Systems (e.g. *Sorghastrum stipoides*, which occurs in high abundances and in Community 5 and sub community 8.2). The terrestrial zones of the PL System (sub community 5.1) are similar to the wet and seasonal zones of both the PL and IDD system (sub community 8.2), and not so much similar to the terrestrial zones of the IDD System (sub community 5.2). This is because the transition between the zones of the open PL System is much more gradual than that of the closed and sharply demarcated IDD System.

As a result of the hydrological regime and gradual zone transition, the zones of the PL System are difficult to delineate with certainty, and display a lot of species overlap. Still there is a strong division between the ‘wet’ zones and the terrestrial zones of the PL System. Zones 1 and 2 occur together as the ‘Sandy Organic Grasslands’ (sub community 8.2), and Zones 3 and 4 occur as the ‘Terrestrial Sandy Grassland’ (sub community 5.1). *Cyperus natalensis* occurred in most of the zones in the PL System, as well as in some IDD communities. *Centella asiatica* occurred abundantly in the wet zones of the PL and IDD Systems, but not at all in the terrestrial zones. These two species together seem to be indicative of some signs of ‘wetland’ conditions on sandy substrates (they were absent in the clay systems).

One of the biggest threats to seasonally wet, event-driven, rainwater-dependent, hygrophilous grasslands such as the PL System is a drop in the water table [9, 36]. This is mostly caused by afforestation, and can already be seen as the numerous informal plots of *Eucalyptus* trees (Figure 10 d). These hygrophilous grasslands are an essential and important part of the wetland catchment area of the Kosi Bay lake system and Lake Sibaya, and are also responsible for the recharge of the lower lying wetland areas such as the Muzi Swamp to the west and the numerous swamp forests occurring in the drainage lines to the east of the PL System [9, 17]. The drop of the water table over the past 20 years have had a significant effect on the PL System, and might explain the floristic and hydrological differences that exist between this system and the other described hygrophilous grasslands on the MCP.

Subsistence agriculture also poses a threat to the wetlands of the PL System (Figure 10 a). These gardens make use of the organic rich and moist soil in the wettest portions of the wetlands. No drainage lines are usually necessary, as the PL System is not permanently wet. Because it is mainly a sedge and grassland system, the vegetation removal to make space for crops is minimal. The effect of the gardens are thus less severe in this system, but a lot of the soil organic carbon still goes lost during the agriculture practices.

6. Conclusion

The results from this study indicate clear differences between the different wetland systems in terms of plant communities and species richness.

The clay systems (PP and DP) have three distinct zones:

- a wet zone (not permanently wet, but saturated for at least 6 months of the year);
- a seasonal zone; and
- a terrestrial zone.

The DP System has more vegetation zones than only three, but they cluster with the hydrological zones set out above.

The sandy and organic wetlands (including the duplex MS System) are characterized by more than three vegetation zones, which can be grouped into a permanently and seasonally wet, and a terrestrial hydrological zone:

- The permanently and seasonally wet zones were found to group together, with the terrestrial zones separately, due to the substrate type.
- The permanently and seasonally wet zones of the wetlands on the MCP are extremely high in organic carbon content, and thus have similar vegetation assemblages.
- The PL System also varies a bit, as there is a lot of overlap from zone 1 to zone 4.

Few of the communities, sub-communities and variants in this study are floristically associated with other vegetation communities described in the literature, probably due to the detailed scale of this wetland study. Although some vegetation studies have been conducted on the MCP, few have focused on wetlands specifically.

The statement by Matthews [31]: '...the important determinants of vegetation communities (are) the interconnected effects of water table (moisture), soil type and topography ...' is supported by this study. Although the specific type of wetland systems add to the various vegetation assemblages found, it does not account for all the differences encountered between vegetation communities. The main difference between vegetation compositions can be accounted for by the substrate type. In the ordination following the removal of the clay substrate type, the main division made was based on substrate (organic versus sand) and hydrological regime (a terrestrial group, and a combined seasonally and permanently wet group (Figure 8)). Although it is unclear at this stage which of these two factors is the main divisive factor, it is deemed unnecessary to investigate in detail as it is known that hydrological regime and organic content of soils are interlinked.

The specific type of system from which a relevé originates is the final classification factor. In certain instances the whole system is characterized by a specific substrate (such as the DP and PP systems), in which case it can be said that their vegetation types are limited to that specific system. The rest of the wetlands on the MCP occur on a predominantly sandy substrate, and

species assemblages will therefore not be limited or exclusive to a specific wetland system (also the reason why the sandy IDD and PL systems are more associated with each other than with the somewhat duplex MS System). Vegetation composition of a specific wetland zone can therefore be influenced and driven on two levels:

1. by the substrate type and hydrological regime; and
2. by the wetland system it occurs in.

Plant species assemblages (communities) and species richness are therefore characteristic for the different wetland zones. However, zone delineation using vegetation composition varies between the different wetland systems in terms of amount and types of zones present, and should be evaluated according to the specific system in question. Not only can the different plant assemblages be used for the successful identification of the different zones within certain wetland types on the MCP, but all could be related to environmental conditions in the field.



Figure 10. Examples of wetland degradation on the MCP with a) cultivation in wetlands in the PL System; b) slash and burn and subsequent cultivation in the swamp forests; c) a destroyed wetland now known as a ‘fossil garden’; and d) one of numerous *Eucalyptus* plantations in a wetland on the MCP.

It is thought that the wetlands on the MCP are currently under stress as a result of drought and intensified forestation and agricultural practices on the MCP. These wetlands, especially the Upland Wetland (PL) System which act as a recharge area for the whole MCP [17], are extremely sensitive ecosystems. In the unprotected areas these wetlands are currently being exploited on a large scale for its goods and services (Figure 10). Human population increases are putting a demand on these resources which cannot be sustained. The Tonga community is dependent on the wetlands on the MCP. However, the current rate of uncontrolled utilization, with the added stress of the *Eucalyptus* plantations, could eventually cause these sensitive wetlands to become totally degraded with resultant loss of plant species and ecosystem functioning.

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