Plant communities of the uMlalazi Nature Reserve and their contribution to conservation in KwaZulu-Natal

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Vegetation research is an important tool for the simplified and effective identification, management and conservation of the very complex ecosystems underlying them. Plant community descriptions offer scientists a summary and surrogate of all the biotic and abiotic factors shaping and driving ecosystems. The aim of this study was to identify, describe and map the plant communities within the uMlalazi Nature Reserve. A total of 149 vegetation plots were sampled using the Braun-Blanquet technique. Thirteen plant communities were identified using a combination of numeric classification (modified Two-way-Indicator Species Analysis) and ordination (non-metric multidimensional scaling). These communities were described in terms of their structure, floristic composition and distribution. An indirect gradient analysis of the ordination results was conducted to investigate the relationship between plant communities and their potentially important underlying environmental drivers. Based on the results, the floristic conservation importance of each plant community was discussed to provide some means to evaluate the relative contribution of the reserve to regional ecosystem conservation targets.

Conservation implications: The uMlalazi Nature Reserve represents numerous ecosystems that are disappearing from a rapidly transforming landscape outside of formally protected areas in Zululand. The descriptions of the plant communities of these relatively pristine ecosystems provide conservation authorities with inventories and benchmarks with which the ecological health of similar ecosystems in the region can be measured.

Introduction

Vegetation research is an important tool for the simplified and effective identification, management and conservation of the very complex underlying ecosystems. Plant community descriptions offer scientists a summary and surrogate for the bewildering combinations of biotic and abiotic factors shaping and driving ecosystems. In response to a recent request by Ezemvelo KwaZulu-Natal Wildlife (EKZNW), this study of the plant communities of the uMlalazi Nature Reserve (uMNR) was conducted as a first attempt to provide such a vegetation description. In order to establish the uniqueness and conservation importance of the uMNR's plant communities, comparisons were made with existing vegetation descriptions from the literature. Without scientifically based ecological information and interpretation of vegetation data, conservation authorities will not be able to either report meaningfully on the state of the vegetation under their management, or set and adapt conservation priorities as required by the *National Environmental Management Biodiversity Act* (Act 10 of 2004) (Von Maltitz, Van Wyk & Everard 1996:188–195).

Previous vegetation studies in the uMNR were conducted at a relatively coarse scale, aimed at providing very general trends within the major vegetation types (Nevill & Nevill 1995:51–58; Todd 1994; Weisser 1978a:95–97). Vegetation maps that were compiled in the past were based on dominant species and vegetation structure classes (Todd 1994; Weisser 1978b). To date, no detailed plant community descriptions based on total floristic composition have been conducted for the uMNR. The only detailed description of these ecosystems comes from the neighbouring Pennington Park by Moll (1972:615–626). Detailed vegetation descriptions for other ecosystems within the Indian Ocean Coastal Belt (IOCB) biome have been published for Tshanini Game Reserve (Gaugris et al. 2004:9–29), Tembe Elephant Park (Matthews et al. 2001:573–594), Lake Eteza Nature Reserve (Neumann, Scott, Bousman & Van As 2010:39–53) and Sileza Nature Reserve (Matthews et al. 1999:151–167). Other detailed plant ecology studies have focussed on foredune advancement, dune vegetation changes and changes in grassland communities (Weisser 1978a:95–97; Weisser, Garland & Drews 1982:127–130; Weisser & Muller 1983:661–667).

Note: Additional supporting information may be found in the online version of this article as Online Appendix 1: https://doi.org/10.4102/koedoe.v60i1.1449-1 and Online Appendix 2: https://doi.org/10.4102/koedoe.v60i1.1449-2

Study area

The uMNR (28°56'S, 31°46'E) is situated directly south of Mtunzini, within the northern half of KwaZulu-Natal, in the southern section of Zululand, South Africa (Todd 1994; Traynor et al. 2010). This coastal reserve (1469 ha) forms part of the Maputaland-Pondoland-Albany Biodiversity Hotspot and the Maputaland Centre of Floristic Endemism (Van Wyk & Smith 2001). The centre contains approximately 2500 infraspecific taxa, of which 9.2% are regarded as near-endemics. The climate of the study area is subtropical with hot, humid summers and mild winters with no frost (Nevill & Nevill 1995:51–58; Todd 1994). The mean annual rainfall fluctuates between 819 mm and 1272 mm, with approximately two-thirds falling in mid-summer and the remaining one-third falling in early winter (Mucina & Rutherford 2006; Tyson & Preston-Whyte 2000).

The ages of the dune fields of the Maputaland coastal plain range from the early Pleistocene (± 5 Ma) to 500 years ago. The dunes of the Maputaland coastal plain are among the most recent geological formations that are found in southern Africa (Gaugris et al. 2004:9–29), with the uMNR beachfront classified as prograding (actively expanding). The soil of the uMNR consists of fine-grained marine sands, typically yellowish or grey apedal soil with early horizon development. The A-horizon is usually thin and enriched with organic matter. Subsoil horizons often show sparse ferruginous mottles. The resulting soil types are classified according to the South African system as mainly cover sands, with some Fernwood soil forms and some very limited Champagne soil formations along the waterlogged bottomlands (Fey 2010:32–35; Matthews et al. 2001:573–594).

This combination of a water-rich environment and highly permeable sandy substrates is the main driver of the vegetation patterns of this biome. The region forms part of the IOCB biome, which is a complex mosaic of zonal, intrazonal and azonal vegetation types (Mucina & Rutherford 2006). The uMNR and its immediate surroundings contain the following major vegetation types: FOz 7 Northern Coastal Forest, FOa 2 Swamp Forest, FOa 3 Mangrove Forest, AZe Subtropical Estuarine Salt Marshes, AZs 3 Subtropical Dune Thicket, AZd 4 Subtropical Seashore Vegetation and AZf 6 Subtropical Freshwater Wetlands (Mucina & Rutherford 2006). Cultivation, afforestation, mining, urban sprawl and invasive alien plants are major threats to the remaining untransformed patches of IOCB vegetation (EKZNW 2009).

Methods

The study area was stratified into homogenous vegetation units using texture and colour classes on aerial imagery (Google Earth 7.1.2.2041 2016). After a reconnaissance of the area to ensure the homogeneity of vegetation units, 149 plots were randomly selected within each of the different homogenous units on the imagery. In the field, however, each sampling plot was critically evaluated according to the first rule of the Zurich–Montpellier sampling method (the placement of the sampling plot should be within a homogeneous vegetation patch that is representative of the perceived plant community). If the sampling plot did not fall within a homogeneous representative vegetation stand, it was moved to the nearest locality that fulfils this criterion. Accessibility to the plot was also taken into consideration.

The Braun-Blanquet sampling method (Werger & Coetzee 1978) was specifically chosen for its international recognition as the most appropriate technique for the description of vegetation when based on total floristic composition (Brown et al. 2013). By using an internationally accepted standard, the data and vegetation description will be compatible and comparable with data from other regions and landscapes. Such comparability and compatibility is crucial for the regional and international coordination of vegetation and ecosystem conservation. Based on the recommendations by Brown et al. (2013), plot sizes varied according to the vegetation types sampled (grasslands 9 m^2, salt marshes 25 m^2, wetland vegetation 25 m^2, foredune communities 49 m^2, swamp communities 49 m^2 and forest communities 1000 m^2) and were marked out in the field to ensure consistency. In all sample plots, each plant species was recorded and the cover–abundance value of each species determined using the modified Braun-Blanquet cover–abundance scale: r (very rare, with a negligible cover), + (present but not abundant, with a cover value of < 1% of the quadrat), 1 (numerous but covering less than 1% of the sample area), 2a (covering 5% – 12% of the sample area), 2b (covering 13% – 25% of the sample area), 3 (covering 25% – 50% of the sample area), 4 (covering 50% – 75% of the sample area), 5 (covering 75% – 100% of the sample area) (Brown et al. 2013).

The names of the plant species follow the latest taxonomy, as provided by the South African Biodiversity Institute online from the Plants of South Africa (POSA), which was last accessed at http://www.ville-ge.ch/musinfo/bd/cjb/africa/ on 15 June 2017. Fieldwork was conducted during the peak growing season (October 2014 – February 2015). The vegetation structure was recorded and described based on the height and canopy cover of the different strata (tall trees, short trees, shrubs, lianas and herbaceous strata) within each plant community and classified in accordance with Edwards' structural classification (Edwards 1983:705–712).

The phytosociological data were captured in TURBOVEG (Hennekens & Schaminee 2001:589–591), where relevés were created and exported as a Cornell condensed format file into JUICE 7.0.84 (Tichy 2002) for analysis. The modified Two-way-Indicator Species Analysis (TWINSPAN) algorithm as contained within JUICE (Tichy 2002) was used to classify the floristic data. The classification of different plant communities was based on total floristic composition, with pseudo-species cut levels set at 0, 1, 5, 12, 25, 50 and 75. Before the classification was performed, all relevé cluster sizes were standardised in order to remove phi coefficient dependence on cluster size.

The fidelity of species to the various plant communities was calculated using the phi coefficient. Fisher's exact test was used to calculate the statistical significance ($p > 0.001$) of the fidelity values calculated for each species. The diagnostic values of species were based on their fidelity to each community, with phi coefficient threshold values set at > 33% (Chytrý et al. 2002:79–90), while dominant species were identified based on their relative cover–abundance within each of the resulting plant communities.

An ordination of the floristic data was performed using a non-metric multidimensional scaling (NMDS) within PC-ORD (McCune & Mefford 1999) in order to visualise dissimilarities between samples in a two-dimensional scatter plot. Environmental data gathered during the vegetation surveys were mostly qualitative descriptions of the physical parameters associated with the various sample sites. At each sample site, attention was focussed on those environmental variables that were deemed more influential with regard to driving vegetation composition and structure. A conscious decision was therefore made to gather detailed environmental data specific and relevant to each sample site, and not a standardised matrix of generalised environmental parameter data. For this reason, it was decided that an indirect gradient analysis would be attempted, based on the detailed sample site descriptions, instead of a direct gradient analysis based on generalised and often irrelevant environmental parameters. All the observations were made based on field testing, with no laboratory testing conducted. The following scales were used to ensure robust and reliable categories for the environmental variables recorded:

- percentage of soil clay content (sausage texture method): < 10, 10–14, 15–19, 20–34, 35–55, > 55
- water drainage from the soil column based on soil texture: fast, medium, slow, stagnant
- water drainage from the landscape based on runoff potential: fast, medium, slow, stagnant
- soil moisture: saturated, moist, dry
- soil salt content (electrical conductivity): high (oceanic saltwater contamination), low (no oceanic saltwater contamination)
- organic content of soil (visual recognition of fibre particles): high (> 10% of horizon volume), some (< 10%), none
- anthropogenic disturbance levels: high, moderate, low, none
- wind exposure: high, medium, low
- sunlight penetration to lower vegetation strata: full shade (> 80%), partial shade (40% – 79%), highly exposed (< 40%).

Plant community names were assigned following the guidelines suggested by Brown et al. (2013), namely, a diagnostic species followed by a dominant species followed by a structural or landscape description. The mapping of the plant communities was performed using Google Earth 7.1.2.2041 (unprojected) and the final output was compiled in Quantum GIS 2.14.1.

Ethical considerations

A plant collection permit (OP 4829/2014) for identification and herbarium preparation was obtained from Ezemvelo KwaZulu-Natal Wildlife (EKZNW) for use in the uMlalazi Nature Reserve.

Results

Classification

The results from the modified TWINSPAN classification and the NMDS ordination are presented in a dendrogram (Figure 1), an ordination scatter plot (Figure 2), a synoptic table (Online Appendix 1) and a full phytosociological table (Online Appendix 2). The environmental parameters associated with the segregation of the various relevé clusters are presented as part of the classification dendrogram (Figure 1). The results from the indirect gradient analysis superimposed on the NMDS ordination scatter plot are presented in Figure 2. Based on the combined results from the modified TWINSPAN classification and the NMDS ordination of the uMNR vegetation, 13 different plant communities were identified:

- *Salicornia meyeriana–Avicennia marina* salt marsh community
- *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest
- *Phragmites australis–Juncus kraussii* saline wetland
- *Scaevola plumieri–Gazania rigens* foredune community
- *Typha capensis–Cyperus dives* wetland community
- *Digitaria eriantha–Dactyloctenium australe* secondary coastal grasslands
- *Stenotaphrum secundatum–Phragmites australis* temporary wetlands
- *Passerina rigida–Carpobrotus dimidiatus* dune scrub community
- *Adenopodia spicata–Vachellia robusta* riverine woodland community
- *Albizia adianthifolia–Trichilia emetica* disturbed coastal dune forest
- *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin
- *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest
- *Carissa bispinosa–Mimusops caffra* climax coastal dune forest.

Representative photographs of the various plant communities are presented in Figure 3.

Ordination

The NMDS ordination (149 relevés) resulted in a scatter diagram with nine distinct clusters when viewed as a two-dimensional plot along axes 1 and 2 (Figure 2). The indirect gradient analysis superimposed onto the scatter diagram revealed the following potential environmental gradients between plant communities, based on the relative distances and sequences among clusters: soil moisture availability, water drainage capability of soils within different parts of the landscape, clay and salt content of soils, effects of fire and grazing, effects of organic content in the upper soil profile and effects of salt-clipping by oceanic salt spray driven by onshore winds.

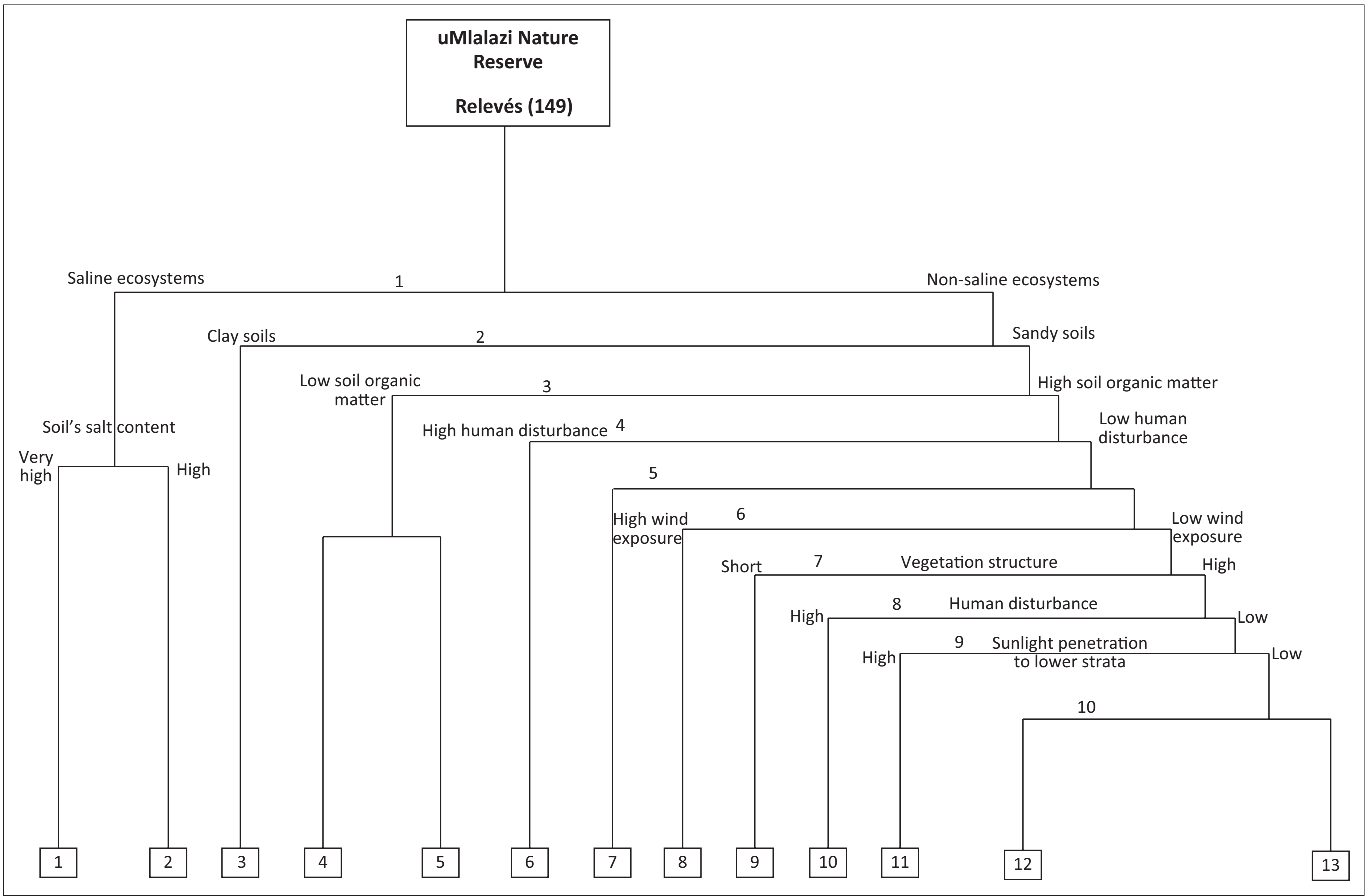
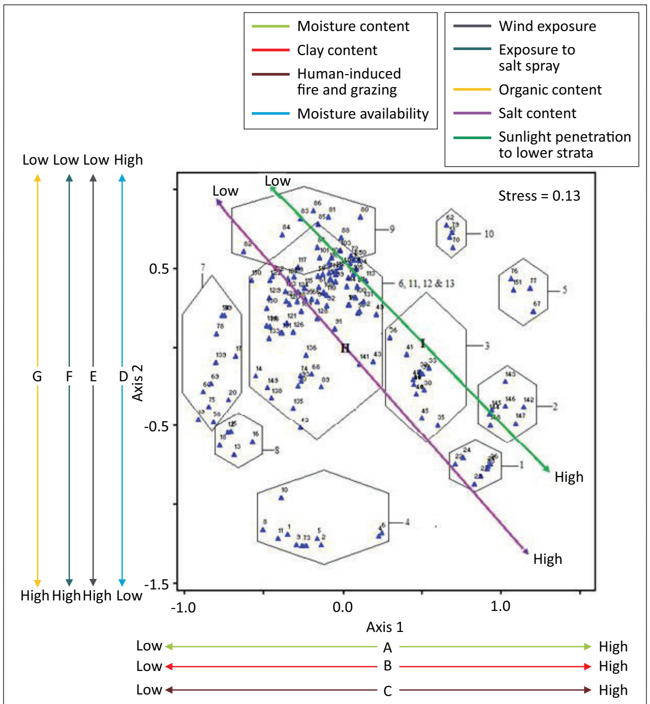


FIGURE 1: Dendrogram illustrating the modified TWINSPAN classification of the vegetation of the uMlalazi Nature Reserve into 13 plant communities.



Note: Relevant environmental gradients were superimposed based on an indirect gradient analysis. Large and small font numbers correspond with plant community and relevé numbers, respectively, while alphabet letters indicate environmental gradients.

FIGURE 2: Plant community clusters of the uMlalazi Nature Reserve as produced by a non-metric multidimensional scaling ordination.

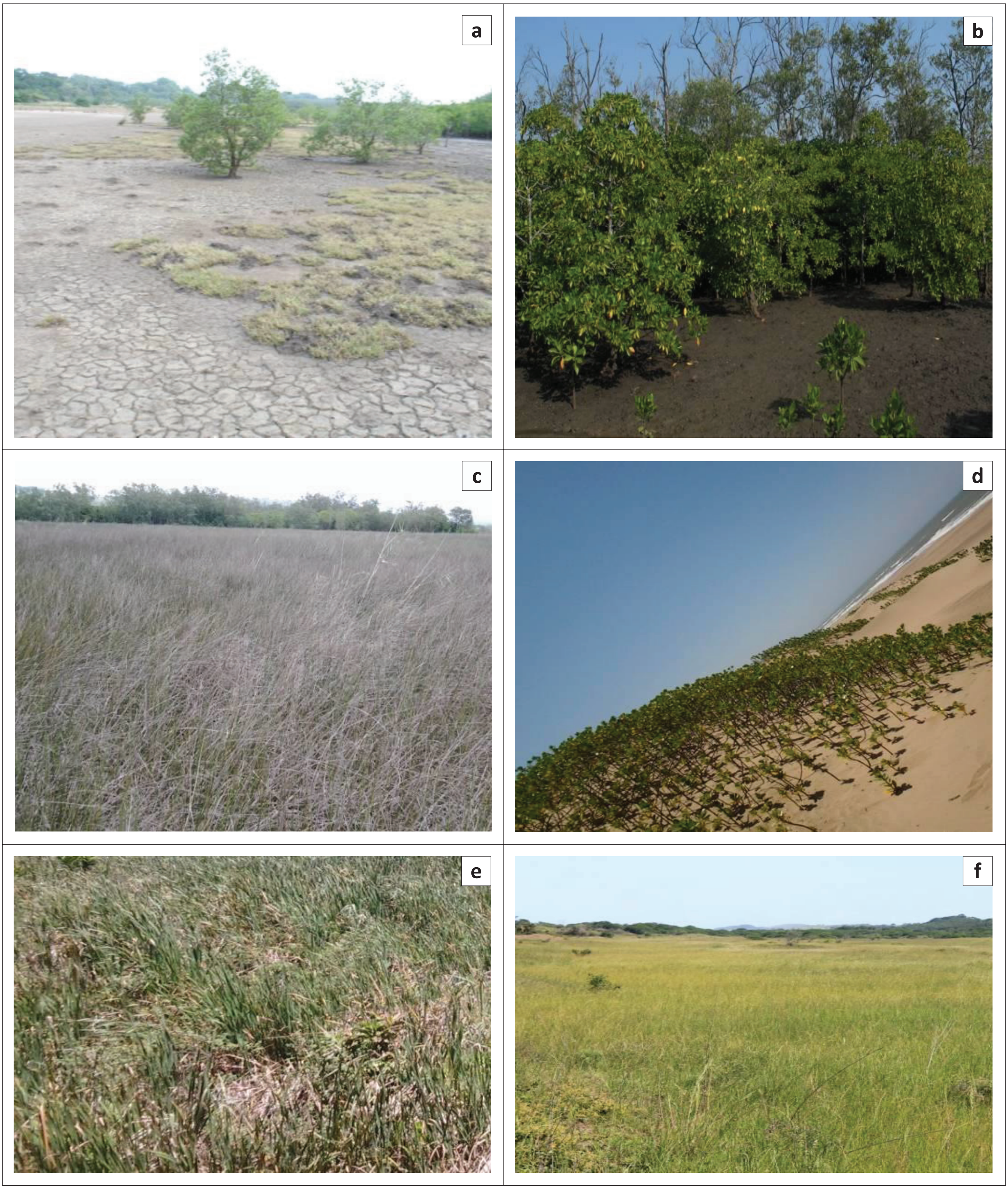
Species richness

The mean species richness per relevé within plant communities is indicated in Figure 4. Plant communities 1–5 show very low levels of species richness and are associated with wetlands and newly formed dunes. These communities can generally be regarded as very harsh to plant life, with only a few specialist species adapted to survive in them. These environmental conditions include soils that are flooded for prolonged periods of time, tidal folding regimes, hyper-saline soils, mobile structureless soils and salt-laden oceanic wind. Plant communities 6, 8, 9, 10, 12 and 13 show relatively high species richness. These plant communities are associated with the more stable soils and more mesic conditions of the sheltered dune forests and grasslands. Communities 9, 10, 12 and 13 revealed the highest species richness in the uMNR.

Plant community descriptions

Plant community 1: *Salicornia meyeriana–Avicennia marina* salt marsh community

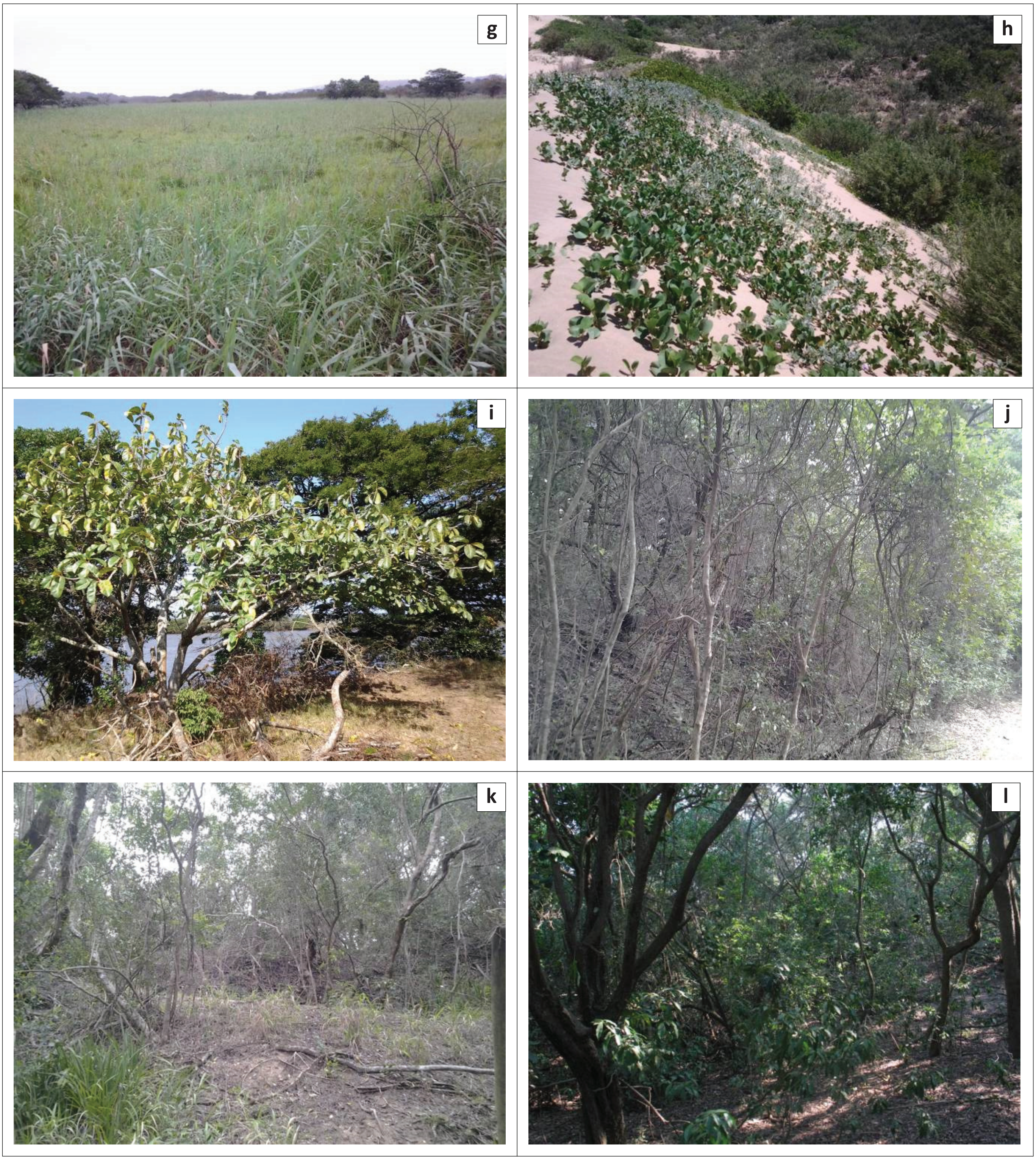
The *Salicornia meyeriana–Avicennia marina* salt marsh community is located within certain estuarine sections of the uMlalazi River floodplains (Figure 5). These sections of the floodplains do not drain freely after the regular seasonal flooding events, and act as natural evaporation pans. The combination of saltwater exposure from tidal movements



Source: (a–l) Photos taken by Nqobile Zungu

FIGURE 3: Representative photographs of the uMlalazi Nature Reserve plant communities: (a) *Salicornia meyeriana–Avicennia marina* salt marsh community, (b) *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest, (c) *Phragmites australis–Juncus kraussii* saline wetland, (d) *Scaevola plumieri–Gazania rigens* foredune community, (e) *Typha capensis–Cyperus dives* wetland community, (f) *Digitaria eriantha–Dactyloctenium australe* secondary coastal grasslands, (g) *Stenotaphrum secundatum–Phragmities australis* freshwater wetland, (h) *Passerina rigida–Carpobrotus dimidiatus* dune scrub community, (i) *Adenopodia spicata–Vachellia robusta* riverine woodland community, (j) *Albizia adianthifolia–Chromolaena odorata* disturbed coastal dune forest, (k) *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin, (l) *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest, (m and n) *Carissa bispinosa–Mimusops caffra* climax coastal dune forest.

Figure 3 continues on the next page →



Source: (a–l) Photos taken by Nqobile Zungu

FIGURE 3 (Continues ...): Representative photographs of the uMlalazi Nature Reserve plant communities: (a) *Salicornia meyeriana–Avicennia marina* salt marsh community, (b) *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest, (c) *Phragmites australis–Juncus kraussii* saline wetland, (d) *Scaevola plumieri–Gazania rigens* foredune community, (e) *Typha capensis–Cyperus dives* wetland community, (f) *Digitaria eriantha–Dactyloctenium australe* secondary coastal grasslands, (g) *Stenotaphrum secundatum–Phragmities australis* freshwater wetland, (h) *Passerina rigida–Carpobrotus dimidiatus* dune scrub community, (i) *Adenopodia spicata–Vachellia robusta* riverine woodland community, (j) *Albizia adianthifolia–Chromolaena odorata* disturbed coastal dune forest, (k) *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin, (l) *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest, (m and n) *Carissa bispinosa–Mimusops caffra* climax coastal dune forest.

Figure 3 continues on the next page →

and the evaporation of water from the temporary pans lead to the hyper-accumulation of salt in the soil of this plant community. These alluvial soils generally contain large percentages of silt, with very little organic matter. The community has a very low vegetation cover and a simple vegetation structure. Its structure varies from open (10%) to patches of closed (75%), low herbaceous vegetation, mostly clumped into colonies of *S. meyeriana*.

Source: (a–l) Photos taken by Nqobile Zungu

FIGURE 3 (Continues ...): Representative photographs of the uMlalazi Nature Reserve plant communities: (a) *Salicornia meyeriana–Avicennia marina* salt marsh community, (b) *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest, (c) *Phragmites australis–Juncus kraussii* saline wetland, (d) *Scaevola plumieri–Gazania rigens* foredune community, (e) *Typha capensis–Cyperus dives* wetland community, (f) *Digitaria eriantha–Dactyloctenium australe* secondary coastal grasslands, (g) *Stenotaphrum secundatum–Phragmities australis* freshwater wetland, (h) *Passerina rigida–Carpobrotus dimidiatus* dune scrub community, (i) *Adenopodia spicata–Vachellia robusta* riverine woodland community, (j) *Albizia adianthifolia–Chromolaena odorata* disturbed coastal dune forest, (k) *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin, (l) *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest, (m and n) *Carissa bispinosa–Mimusops caffra* climax coastal dune forest.

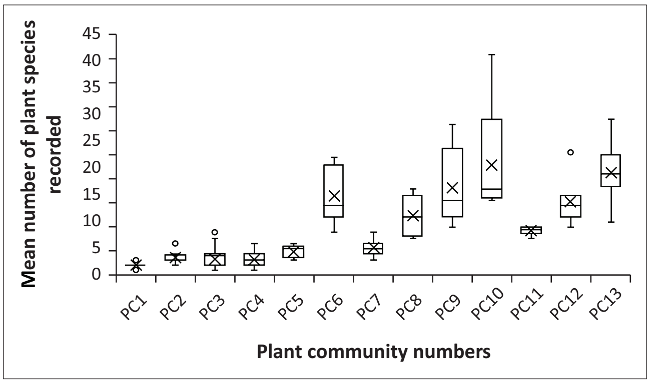


FIGURE 4: Species richness for the 13 plant communities of the uMlalazi Nature Reserve.

The diagnostic species for this plant community, the succulent species *S. meyeriana*, is listed in Species Group (SG A) of the synoptic table (Online Appendix 1). The dominant species for this community are displayed in the full phytosociological table (Online Appendix 2) and include the low-growing halophytic succulent *S. meyeriana* (SG A) and the tree species *A. marina* (SG B). However, *A. marina* has a low cover–abundance value within this plant community. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZe 3 Subtropical Estuarine Salt Marshes, as described by Mucina and Rutherford (2006). Although some authors have described similar subtropical salt marsh vegetation (Colloty, Adams & Bate 2002; Lubke 1997; Venter 1972), no equivalent to that of the uMNR was observed in the literature.

Despite the very low species richness recorded for this plant community (2 ± 0.5 s.d.), its conservation value is considered to be high, based on its unique floristic composition and the unique and dynamic nature of this ecosystem. It acts as a refuge for Benthic organisms during low tides and as rich feeding grounds for many vertebrate species during unusually high tides (Bromberg-Gedan, Silliman & Bertness 2009).

Plant community 2: *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest

The *Bruguiera gymnorrhiza–Avicennia marina* mangrove forest community is restricted to some of the very narrow intertidal zones of the uMlalazi River in the study area (Figure 5). The soils of this community are poorly drained, saline, anoxic and fine-grained. These silt- and clay-rich soils are mostly waterlogged. This community is typically species-poor, dominated by one or two species, and with a dense vegetation cover. Structurally, this community varies from medium to tall, closed mangrove forest (5 m – 8 m).

The diagnostic tree species for this community are *B. gymnorrhiza* and *A. marina* (SG B, Online Appendix 1). The most dominant tree species in this community are presented in the full phytosociological table (SG B, Online Appendix 2) and include the tree *A. marina*, with only a few other visually prominent species such as the perennial sedge *Juncus kraussii.* Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type FOa 3 Mangrove Forest, as described by Mucina and Rutherford (2006). The mangrove community of the uMNR is similar to those described by Moll and Werger (1978), Steinke (1995) and Colloty et al. (2002).

The very extreme and constantly changing environmental conditions of these intertidal ecosystems make them very challenging for terrestrial plant life. Only those plant species that are specifically adapted to deal with both flooded saline conditions, when the tide is in; and extreme desiccation, when the tide is out, are able to colonise these ecosystems.

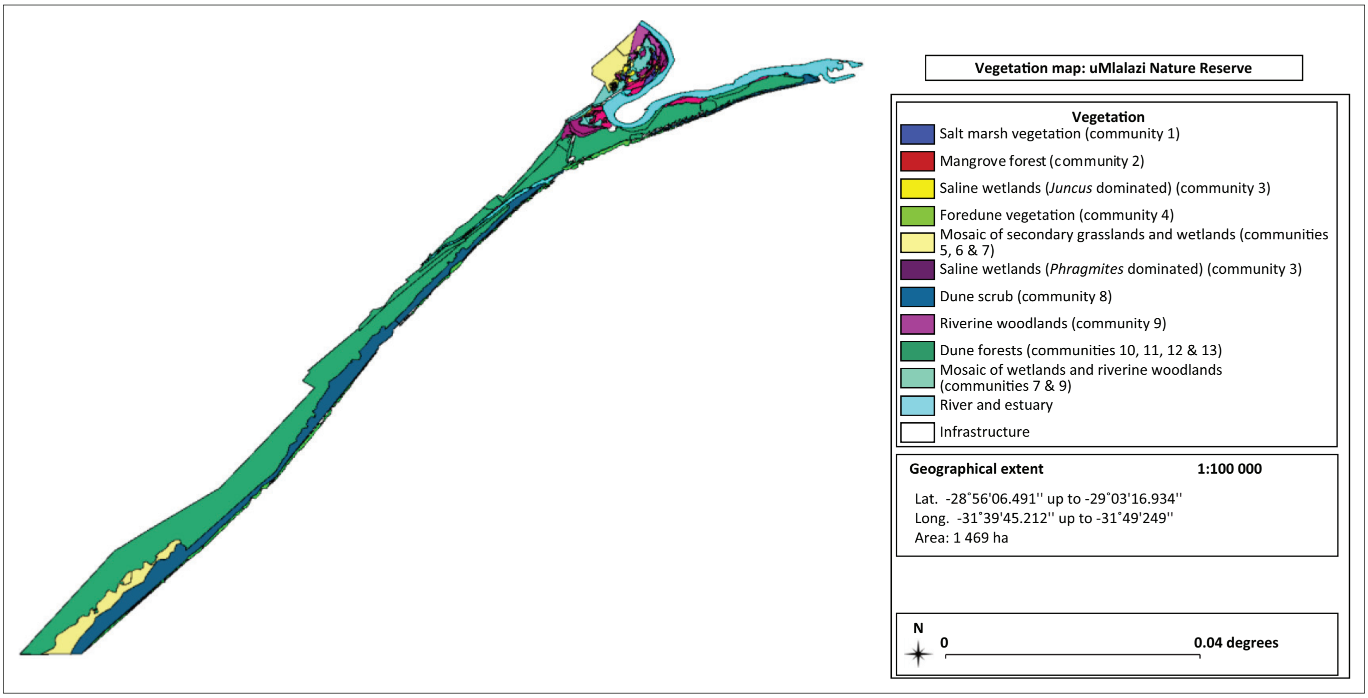


FIGURE 5: Vegetation map of the uMlalazi Nature Reserve.

Without competition from less-adapted plant species, such plant communities become dominated by a handful of specialists, such as mangrove tree species. The conservation value of such plant communities therefore does not lie in its plant diversity, but in its ecosystem functionality.

Plant community 3: *Phragmites australis–Juncus kraussii* saline wetland

The *Phragmites australis–Juncus kraussii* saline wetland plant community occurs within the floodplains of the uMlalazi River in places where saltwater contamination occurs during super-tidal events. It is periodically flushed by freshwater flooding events from the river (Figure 5). Within the floodplains, this community forms a mosaic distribution pattern with the *Salicornia meyeriana–Avicennia marina* salt marsh community. Soils are typically saline, with high silt, clay and organic components. Water drainage is slow and even stagnant in some cases, leading to the accumulation of organic material in these anaerobic conditions. The vegetation is structurally characterised by a medium to tall, closed reed and sedgeland (1.5 m – 3.5 m). The vegetation of this very dynamic ecosystem is regularly harvested of the sedge species *J. kraussii* and the reed species *P. australis* for the weaving and building industry.

The only diagnostic species for this community is the sedge species *J. kraussii* (SG C, Online Appendix 1). The dominant species (Online Appendix 2) include the reed species *P. australis* (SG H), the sedge species *J. kraussii* (SG C), the forb species *Ipomoea cairica* (SG D) and the grass species *Stenotaphrum secundatum* (SG G).

This plant community, with its mosaic of reed and sedge-dominant patches, is the result of fluctuating salinity at both spatial and temporal scales. Wherever and whenever salinity rises, the reed species are negatively affected, and the more salt-tolerant *J. kraussii* outcompetes the reeds. When salt is flushed from the system, the reeds gain the competitive advantage and outcompete *J. kraussii*. The relatively high cover–abundance values recorded for the grass species *S. secundatum* are regarded as an artefact of the drought conditions that prevailed at the time when surveys were conducted. Under more normal flood conditions, this grass species would be drowned, only occupying the better drained fringes of these wetlands. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZe Subtropical Estuarine Salt Marshes, as described by Mucina and Rutherford (2006). *Juncus kraussii*-dominated saline sedgelands occur widely, spread along the estuaries of the east coast of South Africa (Colloty et al. 2002; Taylor, Adams & Haldorsen 2006). Just like in the uMNR, these communities are dynamic in their response to fluctuations in salinity.

Plant community 4: *Scaevola plumieri–Gazania rigens* foredune community

The *Scaevola plumieri–Gazania rigens* foredune plant community occupies the seaward side of the first dune above the high-water mark along the beach (Figure 5). At this point in the landscape the sand is still very mobile and contains virtually no organic matter as yet. Water drainage is fast and salinity is relatively high because of oceanic salt spray. The vegetation structure is relatively simple, with mainly one layer of herbaceous plants with an average height of 0.4 m. As a result, the vegetation structure for this community can be described as patches of low, closed herblands, with large stretches of open, uncolonised mobile sand between the vegetation patches.

The diagnostic species for this plant community include the succulent shrublet *S. plumieri* (SG D Online Appendix 1), the perennial trailing herb *Ipomoea pes-caprae* (SG D) and the creeping perennial herb *G. rigens* (SG D). The most dominant species in this community (Online Appendix 2) is the creeping perennial herb *G. rigens* (SG D). Other visually prominent species include the forbs *I. pes-caprae* (SG D) and *S. plumieri* (SG D), the succulent forb *Carpobrotus dimidiatus* (SG I) and the shrubs *Rhynchosia nitens* (SG I) and *Chrysanthemoides monilifera* (SG I).

Although the recorded species richness is relatively low, this plant community plays a very important ecological role in stabilising the prograding (expanding) beaches of Zululand. This can be seen as the first in a long series of successional stages from dune colonisation to the final climax state of mature coastal dune forest. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZd 4 Subtropical Seashore Vegetation, as described by Mucina and Rutherford (2006). Plant communities and vegetation types similar to the one described for the uMNR occur along large sections of the Zululand coast and have been described by Lubke et al. (1997).

Plant community 5: *Typha capensis–Cyperus dives* wetland community

The *Typha capensis–Cyperus dives* wetland community occurs in interdune depressions where groundwater breaks the surface to form perennial wetlands of various sizes (Figure 5). The sandy soils are waterlogged and contain high percentages of clay particles (30%) and very high percentages of organic matter (> 10%). No distinction was made between groundwater and surface water sources within these highly permeable sandy substrates. The structure of this community can be described as a tall, closed reedland (2 m – 4 m), with a cover value of > 85% at the height of the growing season.

The diagnostic species for this plant community (SG E, Online Appendix 1) include the perennial sedge *C. dives*, the forb *Persicaria serrulata*, the bulrush *T. capensis*, the fern *Cyclosorus interruptus* and the palm *Phoenix reclinata*. The aforementioned species were, incidentally, also recorded as the most dominant in terms of cover–abundance values (SG E, Online Appendix 2). Such patterns of low species richness coupled with an equally low evenness of dominant species are very typical of wetland ecosystems where only specially adapted species can compete for the available resources. As with many South African wetlands, the conservation value of the associated plant community does not lie in its floristic diversity or uniqueness, but rather in its ecosystem functionality. Within the southern sections of the uMNR, this plant community has been disturbed and degraded by illegal grazing practised by neighbouring rural communities. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZf 6 Subtropical Freshwater Wetlands, as described by Mucina and Rutherford (2006). Very few vegetation descriptions that are floristically similar to the *Typha capensis–Cyperus dives* wetland community occurring within the uMNR could be found in the literature (Venter 1972). Despite its relatively common occurrence throughout the coastal dune systems of Zululand, it is very common for azonal vegetation types such as this to be overlooked and neglected during conventional mapping exercises.

Plant community 6: *Digitaria eriantha–Dactyloctenium australe* secondary coastal grasslands

The *Digitaria eriantha–Dactyloctenium australe* secondary coastal grassland community includes one section along the southern section of the uMNR and one section of the newly acquired land along the north-eastern border of the uMNR (Figure 5). The southern section was mainly forest and woodlands before being transformed into grassland by human activities. It is characterised by frequent disturbances in the form of fire and cattle grazing induced by the neighbouring human population along the southern border of the reserve. Soils are sandy with low levels of organic content. This fire-suppressed, subclimax plant community has a short, closed vegetation structure. The northern section of secondary grassland is a remnant of grassland transformed by agricultural activities.

The diagnostic species for this plant community (SG F, Online Appendix 1) include the grass species *D. eriantha, D. australe, Sporobolus africanus, Imperata cylindrica* and *Stiburus alopecuroides*, the sedges *Kyllinga alata* and *Cyperus* species and the forbs *Helichrysum ruderale, Rhynchosia caribaea, Wahlenbergia benghalensis* and *Manulea parviflora.* The dominant species (Online Appendix 2) in this community include the grass species *D. australe, S. africanus*, *I. cylindrica* and *D. eriantha* (SG F). Some woody species that occur within this community include the low shrub *Eugenia capensis* (SG N), the straggling shrub *Searsia nebulosa* (SG H) and the dwarf shrublet *Chironia baccifera* (SG H).

In its current state as a fire-suppressed, subclimax plant community, the conservation value of the southern secondary grassland, based on floristic composition, is regarded as relatively low. Although EKZNW strives to conserve as much tropical grasslands as possible, this secondary grassland should not be calculated as part of the proposed target set for grassland conservation. From a plant conservation perspective, it is recommended that this plant community be allowed to return to its climax state of coastal dune forest. The northern grassland, however, with its very different origins, is regarded as potentially very important for conservation, based on its potential recovery towards a tall and dense wet grassland. Its conservation value will predominantly lie in creating habitat for fauna species of potential concern. Based on the vegetation structure and composition, this northern grassland is regarded as a part of the very diverse major vegetation type CB 1 Maputaland Coastal Belt, as described by Mucina and Rutherford (2006). Although no equivalent for this uMNR plant community was found in the literature, Mucina and Rutherford (2006) specifically mentioned the abundance of these secondary coastal grasslands. However, all of them are floristically and structurally very different because of their varied origins and the varied disturbance regimes that created them. Most of them are species-poor and occur as early successional stages.

Plant community 7: *Stenotaphrum secundatum–Phragmites australis* temporary wetlands

The *Stenotaphrum secundatum–Phragmites australis* temporary wetlands community occurs along depressions within the uMlalazi River floodplain where enough surface water accumulates to form temporary wetlands (Figure 5). The alluvial soil contains enough clay to form a water-impermeable layer that prevents water from draining away. This ecosystem is driven by surface water from seasonal flooding events and rain water. It also occurs, to a limited extent, along small interdune sections where fluctuating groundwater levels create temporary wetlands. Depending on the duration and seasonality of each wetland, varying amounts of organic matter accumulate within them.

The vegetation structure can be described as tall, closed reedland (2 m – 4 m), with a cover value of > 85%. However, there is a cyclical alteration of dominance between the grass and the reed component of this wetland community. During high rainfall, soils are waterlogged, promoting reed growth and effectively drowning stoloniferous grass species. During low rainfall, soils tend to be better aerated, promoting the grass component. At the time of the field surveys, Zululand experienced severe drought conditions, with the lowest average annual rainfall in recorded history for the uMlalazi region (SA Weather Service 2017).

The diagnostic species include the grasses *S. secundatum* and *Paspalum dilatatum,* herbs such as *Ipomoea cairica, Hibiscus trionum* and *Cissampelos hirta* and the sedge *Cyperus eragrostis* (SG G, Online Appendix 1). The most dominant species (Online Appendix 2) for this community is the sedge *P. australis* (SG H). Other dominant species include the grass *S. secundatum* (SG G) and the herbs *I. cairica* (SG G), *H. trionum* (SG G) and *Asystasia gangetica* (SG U). Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZf 6 Subtropical Freshwater Wetlands, as described by Mucina and Rutherford (2006). Venter (1972), and Begg and Carser (1988) described similar plant communities and indicated their widespread occurrence within the Zululand region.

Plant community 8: *Passerina rigida–Carpobrotus dimidiatus* dune scrub community

The *Passerina rigida–Carpobrotus dimidiatus* dune scrub community is found along the second and third dunes from the beach (Figure 5). This community is established on young dunes, which have slightly higher organic matter content than beach sand with no vegetation. The vegetation structure can generally be described as low (1 m) coastal scrub and thickets, with an open to closed canopy structure (30% – 90%). The trees and shrubs that grow in this community are dwarfed, with a compact canopy flattened by wind-shearing and salt-clipping on the windward sides of dunes. The more protected leeward slopes of the older dunes, however, are characterised by a significantly taller thicket vegetation (3 m – 4 m). These tall thickets along the leeward sides are regarded as the early stages of forest formation.

The diagnostic species (SG I, Online Appendix 1) with the highest fidelity for this community is the shrub *P. rigida*, which usually grows up to 1.5 m in height. Other diagnostic species in this community include the shrubs *Carissa bispinosa*, *C. monilifera*, *Osyris compressa*, *Brachylaena discolor, Tephrosia purpurea, Dichrostachys cinerea* and *Searsia nebulosa*; the grass *Stipagrostis zeyheri;* the sedges *Kyllinga* species and *Cyperus* species; the perennial trailing succulent *C. dimidiatus;* the forbs *Senecio* species and *Rhynchosia nitens*; the creeper *Abrus precatorius*; and the woody climber *Rhoicissus digitata.*

The dominant species (Online Appendix 2) in this community include *C. dimidiatus* (SG I), the grass *S. zeyheri* (SG I), the sedges *Kyllinga* species (SG I) and *Cyperus* species (SG I), the herbs *Senecio* species (SG I) and *R. nitens* (SG I) and the shrubs *Eugenia capensis* (SG N), *C. bispinosa* (SG Q), *C. monilifera* (SG I), *B. discolor* (SG I), *T. purpurea* (SG I), *D. cinerea* (SG I), *S. nebulosa* (SG I) and *Chironia baccifera* (SG P). Other visually prominent trees in this community include *Mimusops caffra* (SG Q), *Apodytes dimidiata* (SG L), *Kraussia floribunda* (SG R) and *Allophylus natalensis* (SG U). Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type AZs 3 Subtropical Dune Thicket, as described by Mucina and Rutherford (2006). Weisser (1978b), Weisser et al. (1982:127–130) and Donnelly and Pammenter (1983:705–712) also described this widespread plant community at numerous other Zululand locations.

Plant community 9: *Adenopodia spicata–Vachellia robusta* riverine woodland community

The *Adenopodia spicata–Vachellia robusta* riverine woodland community occurs along the better-draining sections of uMlalazi River floodplain (Figure 5). The structure comprises a tall, dense tree layer and a well-developed dense shrub layer. It is associated with deep, fine-textured soils of recent alluvial deposits that are subject to frequent seasonal flooding. The soils drain freely and do not stay waterlogged for extended periods of time. Deep-rooted trees along the riverbank have year-round access to water from this perennial river.

The diagnostic species for this plant community (SG J, Online Appendix 1) include the shrubs *A. spicata, Tricalysia lanceolata, Hibiscus tiliaceus, Canthium inerme, Pavetta lanceolata, Scutia myrtina, Tecoma capensis* and *Clausena anisata*. The diagnostic herbs include *Scadoxus membranaceus, Chenopodium ambrosioides*, *Oxalis droseroides*, *Nidorella undulata* and *Scadoxus puniceus.* The diagnostic trees include *V. robusta* and *Tarenna pavettoides.*

The most dominant species for this community (Online Appendix 2) include the tree species *V. robusta* (SG J); the shrubs *A. spicata*, *H. tiliaceus*, *C. inerme*, *P. lanceolata*, *S. myrtina*, *T. capensis* and *C. anisata;* the herb *Asystasia gangetica;* and the geophytes *S. membranaceus* and *S. puniceus* (SG J). Because of the very dynamic nature of flooding events along this section of the uMlalazi River, the floodplain is highly heterogeneous at both a special and a temporal level. This prohibits the formation of typical Lowveld Riverine Forest (FOa 1) (Mucina & Rutherford 2006). However, we argue that the *Adenopodia* *spicata–Vachellia robusta* riverine woodland community is essentially an early successional stage within the major regional vegetation type. Similar plant communities were described by Whateley and Porter (1983:745–758) further inland along the Nyalazi, Hluluwe and uMfolozi rivers.

Plant community 10: *Albizia adianthifolia–Trichilia emetica* disturbed coastal dune forest

The *Albizia adianthifolia–Trichilia emetica* disturbed coastal dune forest community has weakly developed sandy–loamy soils with a high organic content in the upper layers. The average total cover for this community is 80% and bare patches make up 20% – 25%. Structurally, this community qualifies as a forest. However, because of varying degrees of disturbance to the different vegetation strata, these forests have lost their structural diversity and complexity. Disturbances recorded throughout this community include fire; wind; the presence of charcoal pits, animal traps, footpaths and roads; subtropical storms; the harvesting of timber, firewood and medicinal plants; alien plant invasions; and the slumping of unstable dunes and substrates. Footpaths were particularly widespread throughout the study area, leading to soil erosion.

The diagnostic species for this community include the trees *T. emetica, A. adianthifolia, Euclea natalensis, Erythrina lysistemon, Apodytes dimidiata, Clerodendrum glabrum, Cussonia zuluensis, Trimeria grandifolia, Deinbollia oblongifolia* and *Ekebergia capensis*; the invasive alien shrubs *Chromolaena odorata* and *Lantana camara*; the native shrubs *Rhynchosia totta* and *Searsia nebulosa*; the forb *Bidens pilosa*; and the grass species *Digitaria longiflora* (SG K, Online Appendix 1).

The most dominant species (Online Appendix 2) include the forb *B. pilosa*; the trees *T. emetica* (SG K), *E. lysistemon* (SG K), *A. dimidiata* (SG L), *C. glabrum* (SG K), *C. zuluensis* (SG K), *E. capensis* (SG K), *T. grandifolia* (SG K) and *D. oblongifolia* (SG K); and the shrubs *C. odorata* (SG K), *L. camara* (SG K), *R. totta* (SG K), *S. nebulosa* (SG I) and *E. natalensis* (SG M). Based on the vegetation structure and composition, this plant community is regarded as a middle-to-late successional stage of coastal dune forest within the major vegetation type FOz 7 Northern Coastal Forest, as described by Mucina and Rutherford (2006). Very few descriptions were found in the literature of the middle-to-late successional stages of forest communities before they reach their climax states (Grainger, Van Aarde & Wassenaar 2011; Von Maltitz, Van Wyk & Everard 1996:188–195). However, most of the coastal dune forests within Zululand that occur outside of formally protected areas are in this anthropogenic subclimax state (Berliner 2005).

Plant community 11: *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin

The *Tricalysia sonderiana–Apodytes dimidiata* dune forest margin community occurs along the forest edges. It is demarcated as a narrow band along the forest (Figure 5). It has deep apedal sandy–loamy soils with a high accumulation of organic matter within the upper 150 mm of the soil column. Structurally, this community can be described as a medium-to-tall dune forest.

The diagnostic species for this plant community (SG L, Online Appendix 1) include the small tree species *T. sonderiana* and the tree species *A. dimidiata*. The most dominant species for this community (Online Appendix 2) includes the tree *A. dimidiata* (SG L), which grows best in these well-drained, organic-rich soils of the forest margin. Other dominant species include *Psydrax obovata* (SG R), the shrubs *Euclea natalensis* (SG M), *Kraussia floribunda* (SG R) and *Ekebergia capensis* (SG N) and the fern *Microsorum scolopendrium* (SG S).

This plant community contains surprisingly few plant species (8.3 ± 0.8 s.d.) when compared to the climax dune forest community (19.2 ± 4.9 s.d.). Generally, forest ecotones are relatively species rich, containing species from both the forest and the neighbouring plant community. In retrospect, the anomaly recorded here may very well have been an artefact of incorrect sample site selection. It is recommended that the forest ecotones of the uMNR be mapped and managed as an integral part of the dune forests. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type FOz 7 Northern Coastal Forest, as described by Mucina and Rutherford (2006). No formal plant community descriptions of coastal dune forest margins were found in the literature.

Plant community 12: *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest

The *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest community was recorded between the *Tricalysia sonderana–Apodytes dimidiata* dune forest margin and the *Carissa bispinosa–Mimusops caffra* climax coastal dune forest; as a result, it displays strong floristic affinities towards these plant communities (Figure 5). The soils underlying this community are deep apedal sands, ranging from medium- to course-grained, with a high organic component within the upper 150 mm of the soil column. Structurally, this community is classified as a tall dune forest. The forest canopy is less dense than the climax dune forests because of the absence of very old and large trees with wide canopies. This results in more light reaching the forest floor, leading to a relatively well-developed shrub layer.

The diagnostic species for this plant community include the tree species *P. longifolia* and *Tricalysia capensis,* the straggling shrub *G. arenicola* and the straggling climber *Smilax anceps* (SG O, Online Appendix 1). The dominant species for this community are displayed in the full phytosociological table (Online Appendix 2) and include *Psydrax obovata* (SG R) and *P. longifolia* (SG O). Other dominant species include the tree species *Sideroxylon inerme* (SG T) and *Garcinia gerrardii* (SG T); the climbers *Smilex anceps* (SG O) and *Rhoicissus tomentosa* (SG Q); the shrubs *K. floribunda* (SG R), *G. arenicola*, *Peddia africana* (SG R), *Putterlickia verrucosa* (SG Q) and *C. baccifera* (SG Q); the grass *Panicum coloratum* (SG O); and the geophyte *Dietes* species (SG M).

Based on the lack of older and larger trees normally found in a climax dune forest, this plant community may very well be a younger successional stage of dune forest. Some preliminary investigations showed that there may very well be a correlation between fire scars on old aerial photographs and the distribution of the *Gymnosporia arenicola–Protorhus longifolia* coastal dune forest community. However, the verification of this pattern has not been attempted in this study. This plant community is therefore regarded as a very late successional stage of dune forest within the major vegetation type FOz 7 Northern Coastal Forest, as described by Mucina and Rutherford (2006). Very few descriptions were found in the literature of the very late successional stages of forest communities (Venter 1972; Von Maltitz et al. 1996:188–195). Some authors (Venter 1972; Von Maltitz et al. 1996:188–195) view these very late successional stages of forest communities simply as variants of climax states.

Plant community 13: *Carissa bispinosa–Mimusops caffra* climax coastal dune forest

The *Carissa bispinosa–Mimusops caffra* climax coastal dune forest community is associated with the oldest and more protected dune forests, extending up to the northern edge of the uMNR (Figure 5). The soil underlying this community is deep sandy soil with a very high organic component within the upper 150 mm. Structurally, it can be described as a tall, closed forest.

The diagnostic species for this plant community (SG Q, Online Appendix 1) include the tree species with the highest fidelity values: *M. caffra, Dovyalis longispina, Vepris lanceolata* and *Cussonia spicata.* The diagnostic shrubs and small trees include *C. bispinosa, Putterlickia verrucosa, Brachylaena discolor* and *Bersama lucens.* The diagnostic woody climbers include *Monanthotaxis caffra, Rhoicissus rhomboidea, Dalbergia armata, Rhoicissus tomentosa* and *Dalbergia obovata*. The diagnostic species include the grass *Oplismenus hirtellus,* the geophyte *Dietes* species as well as the orchids *Cyrtorchis praetermissa, Polystachya sandersonii* and *Ansellia africana*.

The most dominant species for this community (Online Appendix 2) include the tree species *M. caffra* and shrub *C. bispinosa* (SG Q). Other dominant species include the trees *Psydrax obovata*, *B. lucens*, *Kraussia floribunda* (SG R), *Ficus natalensis* (SG U), *Sideroxylon inerme* (SG T), *Psydrax obovata* (SG T) and *D. longispina* (SG Q); the shrubs and small trees *Peddia africana* (SG T), *B. discolor* (SG Q), *Grewia occidentalis* (SG U), *P. verrucosa* (SG Q), *Allophylus natalensis* (SG U) and *Carissa macrocarpa* (SG Q); the woody climbers *R. rhomboidea* (SG U), *Asparagus falcutus* (SG U) and *R. tomentosa* (SG Q); the grasses *O. hirtellus* (SG Q) and *Panicum coloratum* (SG U); the geophyte *Dietes* species (SG Q); and the ferns *Microsorum scolopendrium* (SG S) and *Microsorum punctatum* (SG T).

As was expected, the recorded species richness was relatively high (19.2 ± 4.9 s.d.). This community also contains numerous protected plant species, including *M. caffra, S. inerme, C. praetermissa, P. sandersonii, A. africana* and the extremely rare and endangered saprophytic orchid *Didymoplexis verrucosa* (recorded just outside the uMNR). The conservation value of these forests is regarded as very high, based on their floristic composition and ecosystem functionality. They also contribute greatly to the stability of the dune fields of southern Zululand. Based on the vegetation structure and composition, this plant community is regarded as a part of the major vegetation type FOz 7 Northern Coastal Forest, as described by Mucina and Rutherford (2006). Although none of the forest communities described in the literature were based on total floristic composition, similar forest types were recorded by Venter (1972), Weisser (1978b) and MacDevette et al. (1989).

Discussion

The ordination clusters closely resemble the classification groupings of plant communities with relatively unique species assemblages. For heterogeneous vegetation types, such as forests, the ordination patterns were less distinct, reflecting the floristic overlap between such plant communities. When viewing the complex of the forest communities along ordination axes 1 and 3, slightly more defined clustering of the various communities occurred.

The patterns of species richness recorded within the various plant communities are generally what would be expected. Ecosystems that tend to fluctuate between extremes, such as intertidal zones, show relatively low species richness and are dominated by highly adapted stress-tolerant species such as mangrove species. Stable, mesic ecosystems tend towards high species richness levels dominated by competitive species. The ecotonal forest edge community, which was predicted to show the highest species richness, showed surprisingly few plant species. However, the suspicion is that the anomaly recorded here may very well have been an artefact of suboptimal sample site selection.

The indirect gradient analysis from the ordination scatter plot provided some valuable insights into the general trends in plant community affinities to a variety of environmental variables. Based on our deductions, specific environmental drivers of vegetation structure and plant community composition within the uMNR include the soil moisture availability, water drainage capability of soils within different parts of the landscape, clay and salt content of soils, the effects of fire and grazing, the effects of organic content in the upper soil profile and the effects of salt-clipping by oceanic salt spray driven by onshore winds.

The secondary grasslands within the southern sections of the uMNR show very low species richness, and no regional endemic species were recorded. The conversion of forest to secondary grasslands is therefore considered to contribute very little in terms of tropical grassland conservation. These secondary grasslands do not represent any stage or form of the pristine tropical grasslands observed in other nearby reserves under formal protection. However, it must be added that the grasslands and wetlands within the recently acquired northern sections of the uMNR are essentially very different from the secondary grasslands along the southern sections. The northern grasslands are recovering remnants of grasslands after the impact of agricultural activities. These tall, northern grasslands provide very valuable habitat for threatened bird species such as the Eurasian bittern

(*Botaurus stellaris*), African marsh harrier (*Circus ranivorus*), corncrake (*Crex crex*), swamp nightjar (*Caprimulgus natalensis*) and grass owl (*Tyto capensis*). Their conservation status, based on the habitat provided to a wide range of fauna species, is therefore regarded as relatively high.

The climax coastal dune forest sections within the uMNR are species rich, with an even distribution of dominance among the more visually prominent species. Despite the many laws and regulations protecting coastal forests, very few outside of formally protected areas are still in an ecologically healthy condition. In light of the ongoing decimation of forests outside of protected areas within southern Zululand, the dune forests of the uMNR are regarded as forests of very high conservation value.

The riverine woodlands and wetlands within the uMlalazi River floodplain are relatively species poor and no endemic plant species were recorded there. Although these plant communities are not regarded as of very high conservation value based on their floristic composition, they are regarded as very important for ecosystem functioning and stability. However, the recorded levels of invasion by alien plant species within this heterogeneous mosaic of plant communities are of great concern.

The saline and intertidal ecosystems within the uMNR are not species rich, nor do they contain many endemic plant species. However, based on the ecological importance of mangroves and salt flats along tidal rivers, these ecosystems with their plant communities are critically endangered and under very strict formal protection. It is for this reason that the two mangrove tree species recorded in the uMNR, *Bruguiera gymnorrhiza* and *Avicennia marina*, are protected by law. From a sustainable use perspective, the biannual harvesting of materials from the *Phragmites australis–Juncus kraussii* saline wetland offers an important example of how nature reserves can contribute to the controlled use of natural resources.

The relatively unique prograding (extending) dune system along the uMNR provides a classical example of primary succession, the autogenic changes that drive coastal dune succession and the natural rates at which serial stages replace one another.

Conclusion

The described plant communities of the uMNR can be seen as surrogates for the ecosystems underlying them. These plant communities should form the basis for conservation and management planning within the uMNR. They should also be used as benchmarks and reference examples of undisturbed primary vegetation as well as successional stages in plant community development in order to measure the ecological integrity of similar systems within the Maputaland region.

Based on the floristic similarities between the plant communities of clusters of certain vegetation types, such as forest communities, these vegetation units can be managed and conserved as an integral unit. However, the monitoring of vegetation changes should be conducted on the basis of the individual plant communities. While the management of nature reserves can be done at a relatively coarse scale, monitoring should always be done at the finest relevant scale possible.

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Competing interests

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Authors' contributions

N.S.Z. was the main data collector as part of an MSc research project. He contributed to data analysis, interpretations and preparation of the original manuscript. T.H.C.M. was the co-worker and supervisor and contributed to data collection, analysis, interpretations and preparation of the original manuscript and its revision. R.E.M. contributed to literature reviews and comparisons, data analysis, and the editing and preparation of the extensively revised manuscript.

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