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A first syntaxonomic description of the vegetation of the Karstveld in Namibia

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Abstract

Aims: The Karstveld in Namibia has been recognized as an area of high plant diversity. However, this area is also recognised as a hotspot of various forms of degradation including bush encroachment. Minimal baseline data on the composition and diversity of vegetation in this area is available, therefore this paper is a first attempt to rectify this data deficiency. **Study area:** The Karstveld in Namibia is formed around the Otavi Mountain Range in northern Central Namibia, consisting of strongly karstified carbonate bedrock, rising up to 2000 m a.s.l. The Karstveld includes the Ovambo Basin plains with shallow calcrete soils north of the range, up to the Omuramba Ovambo. Because of orographic effects, the area receives some of the highest rainfall in Namibia, with up to 600 mm per year. **Methods:** A set of 889 relevés with 868 species was selected from the GVID ID AF-NA-001 database. A partial data set, using trees, shrubs, dwarf shrubs and grasses only, was used for the classification with modified TWINSPAN. The initial result yielded four main groups, according to which the data was split and further classified. Several vegetation types observed during field surveys were not reflected in the classification results; these were refined using Cocktail with known characteristic species. **Results:** The four main units represented wetlands and grasslands with six associations, a Thornbush savanna – Karstveld transition zone with four associations, Kalahari vegetation with four associations and the Karstveld proper with eight associations. The latter are grouped together as the *Terminalietea prunioides*, with two orders and three alliances recognised under them. We describe 16 associations according to the ICPN. **Conclusions:** Although the associations presented in this paper are clearly defined, there exists a high degree of diversity within these. The Karstveld is also extraordinary species rich within the context of the arid to semi-arid Namibian environment.

Taxonomic reference: Klaassen and Kwembeya (2013) for vascular plants, with the exception of the genus *Acacia* s.l. (*Fabaceae*), for which Kyalangalilwa et al. (2013) was followed.

Abbreviations: ga = annual grass; gp = perennial grass; GPS = Global Positioning System, referring to a hand-held ground receiver; hl = herb layer, containing all hemicryptophytes, therophytes and geophytes, but excluding grasses (*Poaceae*); ICPN = International Code of Phytosociological Nomenclature (Theurillat et al. 2021); MAP = mean annual precipitation; NMS = nonmetric multidimensional scaling (Kruskal 1964); RDL = Red Data List (IUCN Species Survival Commission 2001); s1 = tall shrubs, i.e. multi-stemmed phanerophytes between 1 and 5 m; s2 = short shrubs, i.e. chamaephytes or 'dwarf shrubs' below 1 m; SOTER = Global and National Soils and Terrain Digital Database (FAO 1993); t1 = tall trees, > 10 m; t2 = short trees, between 5 and 10 m; t3 = low trees, i.e. single-stemmed phanerophytes between 2 and 5 m; TWINSPAN = Two Way Indicator Species Analysis (Roleček et al. 2009); WGS84 = World Geodetic System, 1984 ensemble.

Keywords

Braun-Blanquet, Karst vegetation, Karstveld, modified TWINSPAN, Namibia, Otavi Mountains, syntaxonomy, *Terminalietea prunioides*, vegetation classification

Introduction

Although much is known about the flora of Namibia, the assemblage of species in relation to their habitat in specific areas (i.e. "vegetation") is often less well known and understood (Burke and Strohbach 2000; Strohbach 2001). Broad vegetation descriptions as presented by Giess (1998) and Mendelsohn et al. (2002, 2013) provide only limited information on species composition and habitat, and are thus of limited use for land use and conservation planning (Strohbach 2001, 2018). This lack of baseline data also creates problems with monitoring of vegetation condition, as well as the modelling of potential changes in composition in the light of global climate change (Midgley et al. 2005; Scheiter and Higgins 2009; Stewart et al. 2022; L. Naftal et al. unpubl.).

Within the southern African region, mixed attempts have been undertaken to describe vegetation. In east Africa, potential vegetation maps have been published for several countries, at varying levels of detail (Kindt et al. 2011; Lillesø et al. 2011). This includes Zambia and Malawi in the southern African region. Overview vegetation maps have been published for Angola, Botswana and Zimbabwe, yet only few detailed vegetation descriptions have been published (Airy Shaw 1947; Boughey 1961; Teixeira 1968; Ellery et al. 1990; Bekker and De Wit 1991; Timberlake and Nobanda 1993; Timberlake et al. 1993; Bonyongo et al. 2000; Ellery et al. 2003; Murray-Hudson et al. 2011; Revermann et al. 2018; Gonçalves et al. 2021). In contrast, vegetation descriptive work has a long history in South Africa, culminating in the publication of the monograph "The Vegetation of South Africa, Lesotho and Swaziland" (Mucina and Rutherford 2006). Most of the phytosociological work done in South Africa is intended for management of ecosystems, with the described vegetation types forming proxies for these ecosystems (Brown et al. 2013). Accordingly, most such descriptions name the vegetation types informally as "communities". Brown et al. (2013) recommend that formal descriptions are only to be applied to larger, regional studies. Some examples of such studies are those of Bredenkamp and Theron (1991); Bezuidenhout et al. (1994); Winterbach et al. (2000) and Siebert et al. (2002).

In Namibia, a similar approach to vegetation descriptions has been followed. Early attempts to collect baseline information on natural resources for land use and conservation planning purposes were confined to conservation areas, in particular the Etosha National Park, the Waterberg Plateau Park and the Namib-Naukluft National Park (Robinson 1976; Jankowitz and Venter 1987; Le Roux et al. 1988; see also Kellner 1986; Hines 1992). Since the late 1990s, a project has been started to complete this task (Strohbach 2001, 2014b; Strohbach and Jürgens 2010), with several local and regional vegetation descriptions being published (Strohbach and Petersen 2007; Strohbach and Jankowitz 2012; Jürgens et al. 2013; Strohbach 2013, 2014a, 2019, 2021). With this paper, a first syntaxonomic description at reconnaissance scale of the Karstveld in Namibia is presented.

The Karstveld *sensu* Giess (1998) has been recognized as an area of high plant diversity, endemism and even with a proportionally high number of Red Data List (RDL) species (Hofmeyr 2004; Loots 2005; Craven and Vorster 2006). Yet exactly this area is also recognised as a hotspot of bush encroachment, threatening extensive cattle farming in these farming communities (Bester 1998; De Klerk 2004; Mendelsohn et al. 2006). A large proportion of the natural vegetation especially on deeper soils has been transformed into arable lands for grain, vegetable and fruit production, making use of the relative high rainfall in the area, as well as abundant ground water resources (Mendelsohn et al. 2000, 2006; Schneider 2004). Environmental pollution through inappropriate mining practices also threaten the natural vegetation (Mileusnić et al. 2014; Mihaljevič et al. 2015).

Study area

The Karstveld *sensu* Giess (1998) centres around the Otavi Mountain Range between Otavi, Grootfontein and Tsumeb (Figure 1). It extends to the north and east up to the Kalahari sand basin, and the west until it merges into the Mopane savanna. To the south the Karstveld vegetation transitions into the Thornbush savanna (Giess 1998; Strohbach 2002). Swart and Marais (2009) point out that the Karstveld actually extends westward along the limestone and dolomite ridges of the Otavi Group to beyond Opuwo in the Kunene region. For the purpose of this study, we consider only the vegetation of the Karstveld as defined by Giess (1998) and its associated transitional types. The study area covers roughly 25,000 km^2.

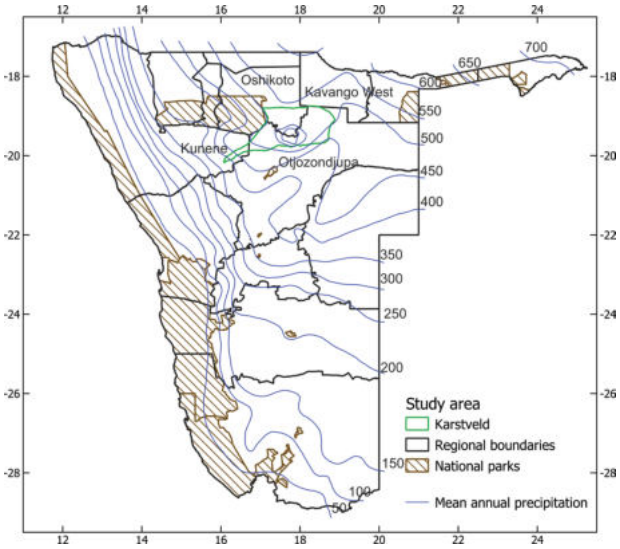

Figure 1. The Karstveld *sensu* Giess (1998) in Namibia. Mean annual precipitation isohyets are superimposed. Data source: NARIS (2001).

Geology and topography

The Otavi Mountain Range forms the northern platform of the Damara Orogenic Belt. A succession of clastic and carbonate sedimentation resulted in four main strata (South African Committee for Stratigraphy 1980; Miller 1997): The lower Nosib Group consists mainly of quartzite, sandstone and conglomerates. This is followed by the Otavi Group, which is divided into the lower Abenab Subgroup and the upper, more massive Tsumeb Subgroup. Within the Abenab Subgroup a variety of different layers exist, including dolomitic rocks. Of note here is the upper Auros formation, which contains a narrow shale band (the "Auros shales") (Pickford 1995; Kamona and Günzel 2007; Bechstädt et al. 2018). The upper Tsumeb Subgroup is formed by massive layers of dolomite and limestone (Pickford 1995; Kamona and Günzel 2007). Due to tectonic movement, three deformation events happened during orogeny, resulting in the forming of an extensive synclinorium (Deane 1995; Schneider 2004; Kamona and Günzel 2007). The mountains raise to above 2000 m a.s.l., or roughly between 500 and 800 m above the surrounding plains (Figure 2). The Otavi Group was topped by younger metamorphized sediments (mostly phyllites, but also slates and sandstones) of the Mulden Group; in most cases these have been eroded away, forming the rich soils of the synclinal valleys (e.g. Otavi Valley) (Miller 1997; Schneider 2004; Kamona and Günzel 2007). In various places, aeolian sand and fine-grained alluvial sediments of the Kalahari were deposited in these synclinal valleys (Schneider 2004). The valleys are extensively used for rainfed or irrigated cropping, exploiting the Karst aquifer, often in conjunction with mines (Schneider 2004; Mendelsohn et al. 2006).

The carbonate rocks of the Otavi Mountains are strongly karstified, forming steep and rough mountain slopes (Schneider 2004; Swart and Marais 2009; Grünert 2013). Although a number of springs are known in the Karstveld, no rivers start here as a result of the Karst landscape (Swart and Marais 2009).

To the south the Otavi Mountain Range transitions into the northern zone of the Damara Orogen (Schneider 2004; Kamona and Günzel 2007). Here the topography is dominated by low ridges and mountains of marbles of the Swakop Group. The upper Ugab valley to the west is covered by unconsolidated Quaternary deposits (Schneider 2004; Grünert 2013), resulting in minimal water flow in these headwaters. Other drainage in the vicinity of the Karstveld is the Omuramba Omatako, passing south-east of the study area. An *omuramba*, plural *omirimbi*, is the local vernacular for a broad, flat, ephemeral watercourse with no discernible riverbed, very low gradient and highly irregular flow, if any (King 1963; Strohbach 2008b). The Omuramba Omumbonde is a tributary to the Omatako, passing north of the Waterberg and collecting water from the Thornbush savanna / Karstveld transition.

To the east, north and west the Otavi Mountain Range tapers out into the plains of the Ovambo Basin, forming part of the greater Kalahari Basin (Miller 1997). The plains are underlain by Cenozoic sediments of the Kalahari Group, in the form of calcretes with shallow soils (ICC et al. 2000; Schneider 2004). These plains drain into the Omuramba Ovambo which starts east of the Kokasib and Gaikos mountains, turns north and later west to discharge in Fisher's Pan as part of the Etosha Pan complex (Strohbach 2008b). The Omuramba Ovambo forms the border to the Kalahari Dune system to the east and north and is regarded as the border of the Karstveld *sensu* Giess (1998).

Climate

The climate of the study area is a typical summer-rainfall, hot, semi-arid steppe (Bsh) following the classification of Köppen (1936). Due to orographic effects, the Otavi Mountain Range receives well over 550 mm mean annual precipitation (Figure 1), whilst the surrounding lowlands receive proportionally less, between 470 mm in the north near Namutoni and 430 mm in the east towards Maroelaboom (Figure 3). The variability of the precipitation is relatively high, with a 26% coefficient of variation (CV) calculated for Tsumeb using the CRU TS4.05 Data set, 1970–2019 (Harris

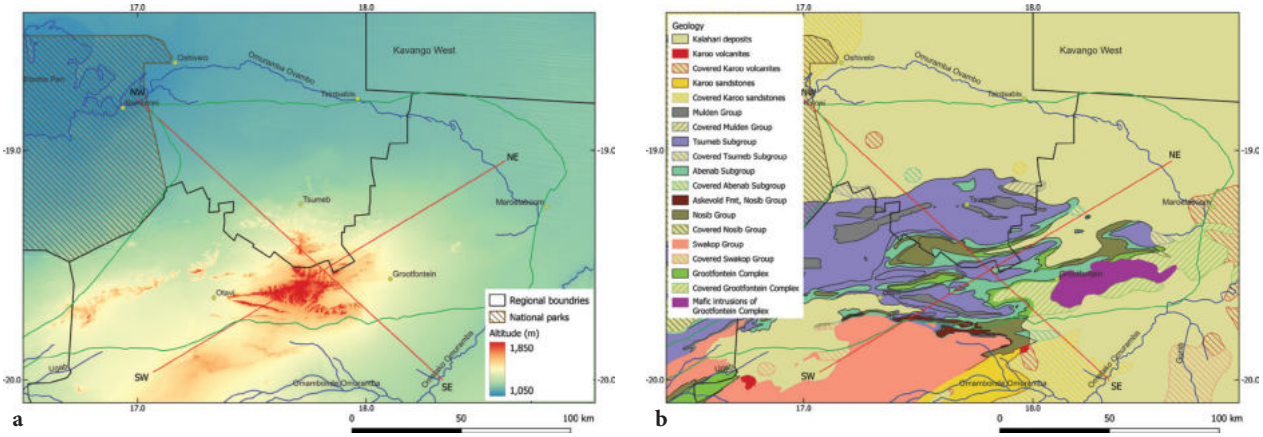

Figure 2. (**a**) Topographical map of the study area; (**b**) simplified geological map of the study area. On these two maps two transects are indicated by red lines. These are presented in Figure 17. Data source: Topography derived from 1 Arc-Second SRTM images (NASA JPL 2013), geological map adapted from the 1:1,000,000 geological map of Namibia (Geological Survey 1980).

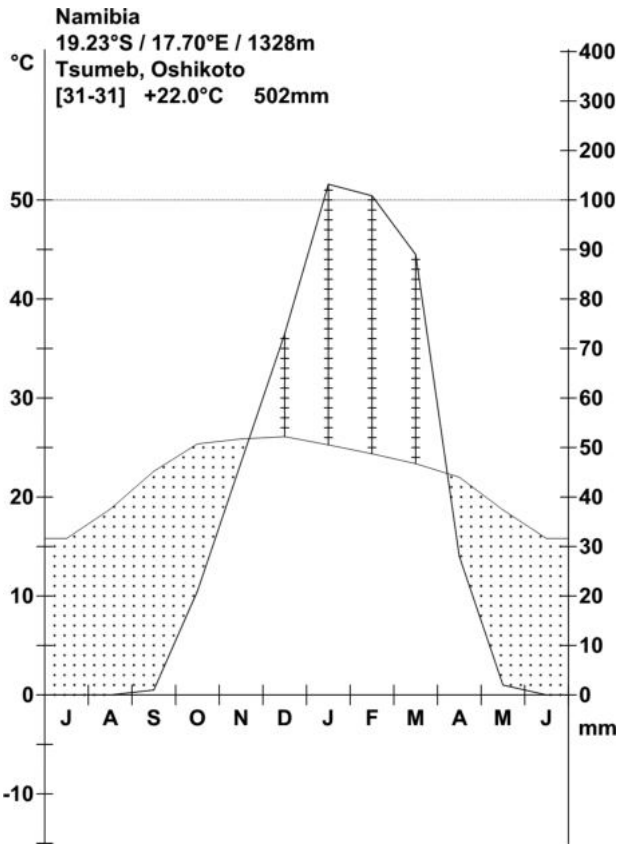

Figure 3. Climate diagram for Tsumeb in the central Karstveld. The diagram follows the scheme of Walter et al. (1975), whilst the data was retrieved from climatecharts.net using CRU TS4.05 data, 1970 – 2019 (Harris et al. 2014; Zepner et al. 2021). Further climate charts for nearby localities within the Karstveld are provided in Suppl. material 1.

et al. 2014). Mendelsohn et al. (2002) estimate the CV on rainfall to be between 30% and 40% for the area.

Average temperatures can raise to between 34° and 36°C during the hottest months, whilst the average coldest temperatures are between 4° and 8°C during winter. Frost can occur; up to 5 days of frost per year are expected (Mendelsohn et al. 2002). The temperatures north of the Otavi Mountain Range are consistently warmer than within and south of the mountains.

Methods

Data selected

A data set of 889 relevés with 868 vascular plant species was selected from the phytosociological database of Namibia (GVID ID AF-NA-001) (Strohbach and Kangombe 2012). Details of the selected data subsets are listed in Table 1. These data are also included in the sPlot database (Bruelheide et al. 2019).

All vegetation data were collected according to the standards of the Vegetation Survey of Namibia, i.e. as regular relevés compiled on a 20 m × 50 m plot (1000 m^2) plot, whilst plot layout was restricted to a specific habitat (Strohbach 2001, 2014b; Strohbach and Jürgens 2010). In cases where the nature of the habitat did not allow a 20 m × 50 m sized plot (e.g. wetland habitats, rock outcrops), the plot shape was adapted to fit the habitat, without reducing the size, nor moving into a different habitat. The size of 1000 m^2 was chosen as suitable for an arid savanna and conforms to size criteria proposed by Brown et al. (2013). Unknown species were collected for identification in the National Herbarium of Namibia (WIND).

Table 1. Overview of data used for this study. All data form part of GVID ID AF-NA-001 (Strohbach and Kangombe 2012) as well as sPlot (Bruelheide et al. 2019). The quality of the rainy season, which has an influence on the growth of the vegetation, was derived according to the criteria of Botha (1998): Normal years had an annual precipitation of between the 40th and 70th percentile of long-term precipitation records, whilst extreme years had below the 10th (extreme dry) or above the 90th percentile (extreme wet) annual precipitation. The evaluation was done using the CRU TS4.05 Data set for Tsumeb, 1970 – 2019 (Harris et al. 2014).

Relevés	Dataset Name	Number	Year	Season quality	Surveyor	Area of interest	Reference (if any)
1301 - 1307	DMP	7 of 422	2004	dry	Marianne Strohbach	South-east of Grootfontein adjacent to Omurambo Omatako	Strohbach (2014)
2259 - 2318	BS-GFT_1999	60	1999	wet	B. Strohbach	Eastern Karstveld	
2772 - 2796	BS_GFT_2003	25	2003	normal	B. Strohbach	Karstveld-Kalahari transition near Maroelaboom	
3183 – 3546 (intermittent)	MS_BIOTA	137 of 558	2001-2002	normal	Marianne Strohbach	Southern edge of Karstveld, transitioning into Thornbush savanna	Strohbach (2002)
3813 – 4066 (intermittent)	North-Kal	131 of 344	1991-1992	normal very dry	B. Strohbach	Eastern Karstveld including Omuramba Ovambo and transition to Kalahari	
4259 - 4350	Uitkomst_9597	92	1995 & 1997	very dry dry	B. Strohbach	John Pandeni Research Station near Grootfontein	
7683 - 7829	BS_GFT_2007	147	2007	normal	B. Strohbach	North-east and south of Grootfontein	
7830 - 7869	BS_Sargberg_2008	40	2008	normal	B. Strohbach	Farm Sargberg near Otavi	Strohbach (2008)
7902 - 8151	BS_Oshikoto_2008	250	2008	normal	B. Strohbach	Central and western Karstveld up to Etosha border	

For the initial relevés done in 1991/92 (data subset North-Kal), no GPS was available, and the position was determined using 1:50 000 topographic map series of Namibia. Later plot positions could be determined by GPS, initially using the old Schwarzeck reference standard (Merry and Wackerle 2006); as from 2004 the WGS 84 reference system was used. As habitat descriptors the landscape type, local topography, slope and aspect, local lithology (i.e. base material for soils), stone cover and disturbance were noted, using the SOTER scheme (FAO 1993). Only for few relevés soil samples (topsoil and B-horizon) were collected and analysed in the Agriculture Laboratory of the Ministry of Agriculture, Water and Forestry. Standard analytical procedures were followed (Pansu and Gautheyrou 2006). Additional habitat data was derived from GIS maps based on the position of the survey plots; this included the estimated annual precipitation (NARIS 2001), altitude (NASA JPL 2013), stratigraphy (i.e. the underlying geology) (Geological Survey 1980) and general soil classification (ICC et al. 2000).

Classification procedures

The combined data was imported into Juice (Tichý 2002), and the different layers of species were combined (i.e. structural information was not used in the classification). Likewise, different subspecies and varieties of a species were combined (e.g. *Senegalia mellifera* and *Senegalia mellifera* subsp. *detinens*; *Stipagrostis uniplumis* and *Stipagrostis uniplumis* var. *uniplumis*), unless such subspecies or varieties were known to have distinct different ecological traits and were clearly differentiated in all subsets (e.g. *Melinis repens* subsp. *repens* (perennial) vs. *Melinis repens* subsp. *grandiflora* (annual)). As *Vachellia reficiens* (Wawra & Peyr.) Kyal. & Boatwr. and *Vachellia luederitzii* (Engl.) Kyal. & Boatwr. are very closely related and easily confused during field observations, and both these species occurred in the study area (potentially even together in the same stand) (Schreiber et al. 1970; Mannheimer and Curtis 2009), these have been combined in the classification data set and referred to as "*Vachellia reficiens* / *luederitzii*". The final cleaned data set consisted of 889 relevés with 867 species.

A partial data set comprising trees, shrubs, dwarf shrubs and grasses only, was prepared from the original complete relevés. This resulted in a matrix with 306 species only. This data set reduction was done to avoid confusions with incorrect field identifications over various seasons, composition differences due to seasonal variations and general 'observer bias' of especially the ephemeral (herbaceous) component of the vegetation. This reduced data set was used for the classification procedure.

An initial classification was done using modified TWINSPAN (Roleček et al. 2009), with average Sørensen as distance measure, but without using pseudospecies. This classification resulted into four clusters, which were interpreted as representing (i) wetlands and associated grasslands, (ii) a transition zone between the Thornbush savanna and the Karstveld (both *sensu* Giess 1998), (iii) Kalahari type vegetation on deep aeolian sands and (iv) the true Karstveld types. This classification result was used to split the data set into four subsets for further classification, again using the modified TWINSPAN classification algorithm and always using average Sørensen as distance measure. The level of splitting was determined using peaks in crispness values (Botta-Dukát et al. 2005).

The classification of the clusters using partial data was transferred to the full data set. During analysis of the resulting clusters some subdivisions were found to be not ecologically interpretable; thus such branches were merged for an ecological interpretable result. Also, some of the grasslands were found to be classified with the Thornbush savanna. Likewise, a wetland type was classified within the true Karstveld types. These groups were manually moved to Cluster 1 (Wetlands and Grasslands) for easier interpretation. It was also realised that some vegetation types observed during field surveys were not represented in the classification results. To rectify this, a refinement of the classification results was done using Cocktail procedures (Bruelheide and Flintrop 1994; Bruelheide 1997). A detailed account of these Cocktail refinements is presented in the Results section of this paper.

Once an ecologically interpretable result was achieved, phytosociological tables were compiled and the synopsis for various associations extracted. Diagnostic species were determined and sorted using the phi coefficient of association (Chytrý et al. 2002), calculated separately across each subcluster (i.e. for the wet- and grasslands, the Thornbush – Karstveld transistion, the Kalahari and the true Karstveld). For this calculation the numbers of relevés were standardised following Tichý and Chytrý (2006). Species with phi ≥ 0.4 were considered as diagnostic and with phi ≥ 0.6 as highly diagnostic (indicated in bold in the synopsis); however, species with a non-significant fidelity at $\alpha = 0.05$ using Fisher's exact test were omitted. Species occurring with at least a 60% frequency were regarded as constant and with at least 80% frequency as highly constant (also indicated in bold in the synopsis).

The resulting terminal units were formally described as associations according to the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021), unless, due to low numbers of sampled relevés, the validity of such units as unique associations could not be established with certainty. In these cases, the units are treated informally as "communities". All habitat descriptions follow SOTER and/or the Namibian soil map (FAO 1993; ICC et al. 2000).

Further descriptors of the associations

The average cumulative cover values of the trees, shrubs, dwarf shrubs, perennial grasses, annual grasses and forbs was calculated based on the available growth form

data. Structural descriptions follow Edwards (1983). The average species richness in 1,000 m² per association or community was calculated from the full relevé data. A count of all species within an association or community was taken as the observed Gamma diversity. In addition, an estimate of potential species richness for the association or community was calculated with a first-order Jackknife as proposed by Heltshe and Forrester (1983) and Palmer (1990).

As bush encroachment is a topic in the current study area, Simpson's Dominance Index and Smith-Wilson's Index (E_{var}) (Peet 1974; Smith and Wilson 1996) were calculated for each relevé using Juice (Tichý et al. 2011). Frome these, box-and-whisker plots were constructed per association described.

Environmental gradients

From the original data set, a subset consisting of relevés of the Thornbush – Karst transition, Kalahari and Karstveld (clusters 3, 4 and 5) was compiled for importing into PC-Ord 7.02 (McCune and Mefford 2016). The wetlands and grasslands were not used in this analysis as these are specialized habitats and likely to be outliers in an ordination, confounding the interpretation of relationships within the main savanna types. This data set consisted of 852 relevés and 813 species. Together with this, an environmental data set was compiled, consisting of the following quantitative variables: altitude, slope class, gravel, small, medium, large stone, rock cover (in classes, following SOTER (FAO 1993)), estimated soil depth, mean annual precipitation, observed number of species and sandiness of the soils. This latter variable was derived from the soil type: rock outcrops and leptic Regosols were classed 1; mollic Leptosol associations classed 2; Cambisol associations classed 3; Fluvisols and Arenosols / Calcisols combinations 4, whilst pure Arenosols were classed 5. Missing data for stone cover and slope class was extrapolated by calculating a median value for each variable for the respective association. In addition, the vegetation association, broad vegetation class (i.e. cluster), geology, landscape and soil type were added as categorical variables.

This data set was used to calculate an NMS ordination (Kruskal 1964), using average Sørensen dissimilarity as distance measure. The ordination was calculated in three dimensions, based on an initial scree plot of stress versus dimensions (McCune et al. 2002; Peck 2010). The solutions were calculated with 200 iterations using real and 249 runs using randomised data for a Monte Carlo test. To aid the interpretation of the resulting scatter plots of the ordination results, the environmental variables were overlain as a joint plot onto a scatter diagram of the plots, with an r^2 cut-off level of 0.100. Using PC-Ord's species-contouring feature, the species distribution for some characteristic phanerophytic species was plotted against these main environmental gradients to illustrate their preferred habitat and distribution.

Results and discussion

Initial classification results

The classification results are depicted in Figure 4. In cluster 2 (Thornbush – Karstveld transition) and in cluster 4 (Karstveld proper) grassland types and a wetland type have been identified respectively; these relevé clusters have been moved to Cluster 1 (Wetlands and grasslands) for easier interpretation.

Within the grasslands associated with the Thornbush – Karstveld transition, two distinct associations were observed during field work, recognisable by different species composition and different habitats These however were not separated by the modified TWINSPAN classification. For this, Cocktail (Bruelheide and Flintrop 1994; Bruelheide 1997) was employed as follows: Relevés belonging to association 2.1.2.1 were selected based on the occurrence of *Themeda triandra*, *Cymbopogon caesius*, *Cynodon dactylon* and *Hyparrhenia hirta.* Relevés belonging to association 2.1.2.2 were selected based on the occurrence of *Brachiaria serrata*, *Cymbopogon pospischilii*, *Jamesbrittenia atropurpurea* and *Euphorbia spartaria.*

Also in the Thornbush – Karstveld transition, thickets with *Olea europea* subsp. *africana* were found in the plains and footslopes of the Otavi mountains. These differed from the thornbush shrublands (association 3.1.1.3) further south through a far denser and higher structure and containing several distinct species not found elsewhere. Although these were not separated using modified TWINSPAN, these were recognised as an association based on their composition and physiognomy. To separate this association from the remainder of the thornbush shrublands, Cocktail was employed, searching for relevés containing *Olea europea* subsp. *africana*, *Enneapogon desvauxii*, *Elaeodendron transvaalensis*, *Fingerhuthia africana*, *Euclea undulata*, *Vachellia karroo* and *Croton gratissimus.* All selected relevés come from the clusters 3.1.1.3.1 and 3.1.1.3.2 and were grouped as 3.1.1.4.

An abbreviated synoptic table, containing only diagnostic and/or constant species, is provided with each major grouping (Tables 2–5). Only for the Karstveld proper (Cluster 4) higher syntaxa are described according to the ICPN. The phytosociological tables for these syntaxa are presented in Suppl. material 2, and the corresponding full synoptic tables in Suppl. material 3. All type relevés are highlighted and reproduced in the phytosociological tables.

1. Ephemeral wetlands

The ephemeral wetlands are characterized by the presence of ***Lagarosiphon muscoides, Nymphoides indica* subsp. *occidentalis,*** *Eragrostis rotifer*, *Panicum gilvum*, *Nymphaea nouchali* var. *caerulea*, *Marsilea nubica* and *Echinochloa* species. The vegetation is dominated by the plant families *Poaceae* (9 species), *Cyperaceae* (6 species) and *Asteraceae* (4 species). Within central and northern

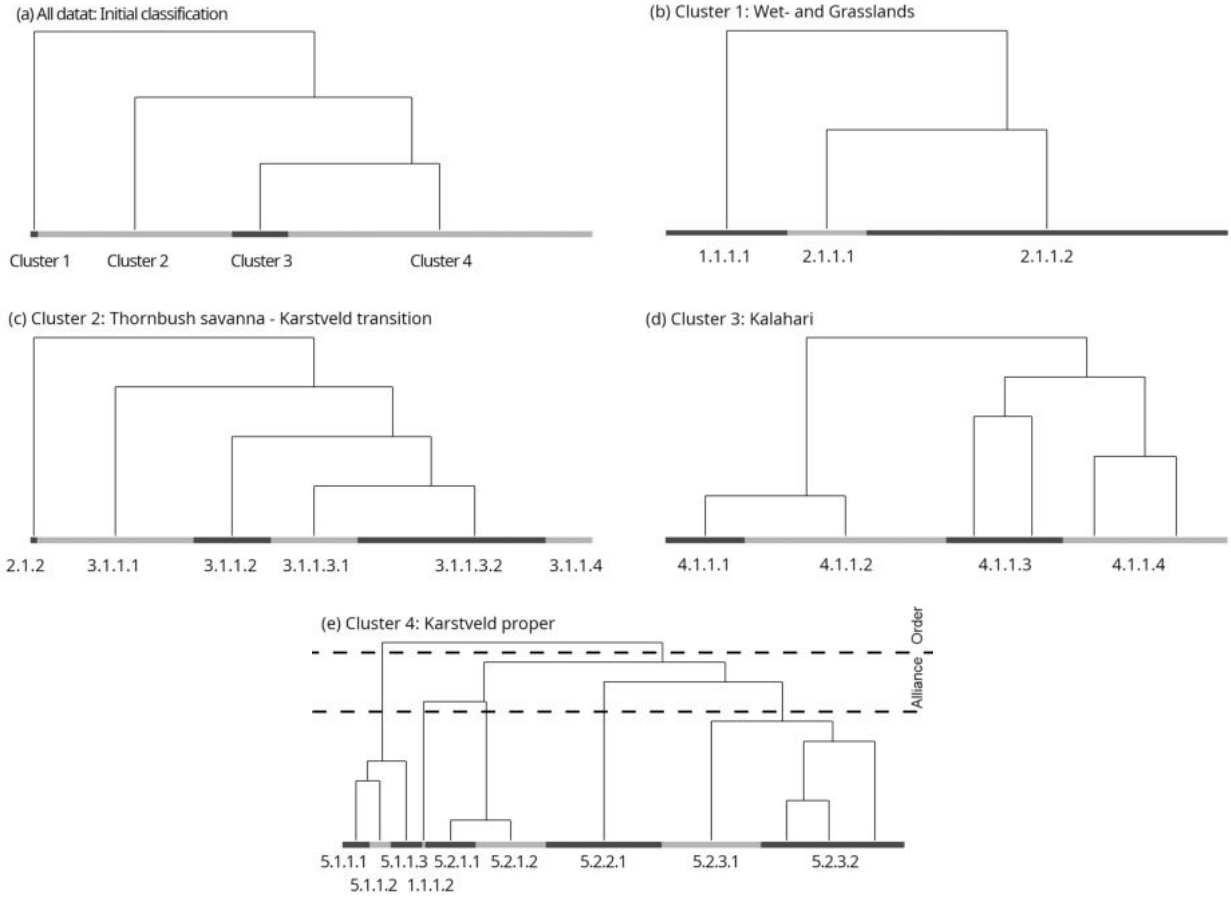

Figure 4. Dendrograms of (**a**) the initial classification of all data, and (**b**) to (**e**) of the individual clusters. Only for the Karstveld proper (*Terminalietea prunioidis*) (**e**) formal higher order syntaxonomic subdivision have been determined; these are indicated by stippled lines.

Namibia, a number of these ephemeral wetlands, locally referred to as *vleys*, are known (Hines 1993; Clarke 1999). Two such communities were identified within the study area. Due to the low number of relevés and pending a full review of these ephemeral wet- and grasslands, no formal description is presented. An abbreviated synoptic table is presented in Table 2, the full synoptic table is available in Suppl. material 3.

Overview of the ephemeral wetlands:

1.1 Undefined upper hierarchy
- 1.1.1.1 *Nymphoides indica-Echinochloa pyramidalis* community
- 1.1.1.2 *Panicum gilvum-Marsilea nubica* community

1.1.1.1 Nymphoides indica-Echinochloa pyramidalis community

Number of relevés: 4
Number of species observed: 22
Estimated number of species: 34
Average species density in 1000 m^2: 9
Diagnostic species: ***Nymphoides indica*** **subsp.** ***occidentalis, Eragrostis rotifer, Nymphaea nouchali*** **var.** ***caerulea, Echinochloa pyramidalis, Cyperus compressus,*** *Lagarosiphon muscoides*

These vleys occur embedded in the Omuramba Ovambo, surrounded by a fringe of *Terminalio prunioidis–Spirostachyetum africanae* (see 5.2.3.1). The vley vegetation is dominated by the aquatic plants *Lagarosiphon muscoides*, *Eragrostis rotifer*, *Echinochloa pyramidalis*, *Schoenoplectus corymbosus*, *Nymphoides indica* subsp. *occidentalis*, *Leptochloa fusca* and *Echinochloa crus-galli***.** The presence of the geophytic hydrophyte *Nymphaea nouchali* indicates that these vleys are generally deeper (about 1 m or more), and regularly filled with water, allowing this species to survive. Similar vleys have been found to the east in the Maroelaboom Dune Belt and the Tsumkwe district (Hines 1993) (Figures 5a, 6a).

1.1.1.2 Panicum gilvum-Marsilea nubica community

Number of relevés: 3
Number of species observed: 14
Estimated number of species: 20
Average species density in 1000 m^2: 7
Diagnostic species: ***Panicum gilvum, Marsilea nubica, Lapeirousia avasmontana, Combretum imberbe,*** *Lagarosiphon muscoides*

The *Panicum gilvum-Marsilea nubica* community is found in feeder streams to the Omuramba Ovambo system, and is dominated by the aquatic species *Marsilea nubica*,

Table 2. Abbreviated synoptic table for the wetlands and grasslands, showing all species occurring in more than 10% of relevés of these groups, with fidelity (phi coefficient x 100) and frequency of occurrence (%).

Higher grouping	**1.1 Wetlands**				**2.1 Grasslands**							
					2.1.1 *Ishana* grasslands				**2.1.2 Mesic grasslands**			
Association	**1.1.1.1**		**1.1.1.2**		**2.1.1.1**		**2.1.1.2**		**2.1.2.1**		**2.1.2.2**	
No of relevés	**4**		**3**		**3**		**11**		**10**		**6**	
Species	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**
Nymphoides indica subsp. *occidentalis*	100	100	---	0	---	0	---	0	---	0	---	0
Eragrostis rotifer	86	100	---	0	---	0	---	18	---	10	---	0
Echinochloa pyramidalis	67	50	---	0	---	0	---	0	---	0	---	0
Cyperus compressus	67	50	---	0	---	0	---	0	---	0	---	0
Nymphaea nouchali var. *caerulea*	67	50	---	0	---	0	---	0	---	0	---	0
Lapeirousia avasmontana	---	0	79	67	---	0	---	0	---	0	---	0
Marsilea nubica	---	0	79	67	---	0	---	0	---	0	---	0
Panicum gilvum	---	0	79	67	---	0	---	0	---	0	---	0
Combretum imberbe	---	50	64	100	---	0	---	0	---	30	---	17
Sporobolus spicatus	---	0	---	0	100	100	---	0	---	0	---	0
Leptochloa fusca	---	25	---	0	87	100	---	0	---	0	---	0
Odyssea paucinervis	---	0	---	0	86	100	---	27	---	0	---	0
Sporobolus acinifolius	---	0	---	0	83	100	---	36	---	0	---	0
Chloris virgata	---	0	---	0	---	0	89	82	---	0	---	0
Willkommia sarmentosa	---	0	---	0	---	0	83	73	---	0	---	0
Sporobolus ioclados	---	0	---	0	---	0	83	73	---	0	---	0
Aristida stipoides	---	0	---	0	---	0	77	64	---	0	---	0
Eragrostis viscosa	---	0	---	0	---	0	71	55	---	0	---	0
Hirpicium gazanioides	---	0	---	0	---	0	71	55	---	0	---	0
Dactyloctenium aegyptium	---	0	---	0	---	67	66	91	---	0	---	0
Sesuvium sesuvioides	---	0	---	0	---	0	57	36	---	0	---	0
Ipomoea coptica	---	0	---	0	---	0	57	36	---	0	---	0
Cyperus atriceps	---	0	---	0	---	0	57	36	---	0	---	0
Commelina subulata	---	0	---	0	---	0	57	36	---	0	---	0
Blepharis leendertziae	---	0	---	0	---	0	57	36	---	0	---	0
Sericorema sericea	---	0	---	0	---	0	52	45	---	0	---	17
Eragrostis trichophora	---	0	---	0	---	0	52	45	---	0	---	17
Microchloa caffra	---	0	---	0	---	0	49	55	---	20	---	17
Xerophyta humilis	---	0	---	0	---	0	49	27	---	0	---	0
Ophioglossum lancifolium	---	0	---	0	---	0	49	27	---	0	---	0
Themeda triandra	---	0	---	0	---	0	---	0	100	100	---	0
Elionurus muticus	---	0	---	0	---	0	---	0	81	70	---	0
Eragrostis lehmanniana	---	0	---	0	---	0	---	0	81	70	---	0
Hilliardiella oligocephala	---	0	---	0	---	0	---	0	77	90	---	33
Ipomoea oblongata	---	0	---	0	---	0	---	0	75	60	---	0
Hypoxis iridifolia	---	0	---	0	---	0	---	0	71	70	---	17
Eragrostis superba	---	0	---	0	---	0	---	0	71	70	---	17
Hermannia depressa	---	0	---	0	---	0	---	0	67	50	---	0
Corchorus asplenifolius	---	0	---	0	---	0	---	0	67	50	---	0
Hermannia eenii	---	0	---	0	---	0	---	0	67	50	---	0
Wahlenbergia undulata	---	0	---	0	---	0	---	0	60	40	---	0
Solanum delagoense	---	0	---	0	---	0	---	0	60	40	---	0
Lantana angolensis	---	0	---	0	---	0	---	0	60	40	---	0
Hyparrhenia hirta	---	0	---	0	---	0	---	0	60	40	---	0
Convolvulus sagittatus	---	0	---	0	---	0	---	0	60	40	---	0
Hibiscus trionum	---	0	---	0	---	0	---	0	60	40	---	0
Pollichia campestris	---	0	---	0	---	0	---	0	55	50	---	17
Andropogon gayanus var. *polycladus*	---	0	---	0	---	0	---	0	55	50	---	17
Cymbopogon caesius	---	0	---	0	---	0	---	0	55	60	---	33
Solanum lichtensteinii	---	0	---	0	---	0	---	0	55	60	---	33
Osteospermum muricatum	---	0	---	0	---	0	---	0	51	30	---	0
Alternanthera pungens	---	0	---	0	---	0	---	0	51	30	---	0
Urochloa oligotricha	---	0	---	0	---	0	---	0	51	30	---	0
Listia heterophylla	---	0	---	0	---	0	---	0	51	30	---	0
Indigofera vicioides	---	0	---	0	---	0	---	0	51	30	---	0
Cynodon dactylon	---	0	---	0	---	33	---	18	50	70	---	17
Setaria pumila	---	0	---	0	---	0	---	0	47	40	---	17
Euphorbia inaequilatera	---	0	---	0	---	0	---	0	47	40	---	17
Urochloa brachyura	---	0	---	0	---	0	---	18	46	50	---	17

Higher grouping	1.1 Wetlands				2.1 Grasslands							
					2.1.1 *Ishana* grasslands				2.1.2 Mesic grasslands			
Association	1.1.1.1		1.1.1.2		2.1.1.1		2.1.1.2		2.1.2.1		2.1.2.2	
No of relevés	4		3		3		11		10		6	
Species	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**
Fingerhuthia africana	**---**	0	---	0	---	0	---	0	---	10	94	100
Cymbopogon pospischilii	**---**	0	---	0	---	0	---	0	---	40	81	100
Geigeria otaviensis	**---**	0	---	0	---	0	---	0	---	0	79	67
Helichrysum cerastioides var. *aurosicum*	**---**	0	---	0	---	0	---	0	---	0	79	67
Jamesbrittenia atropurpurea subsp. *pubescens*	**---**	0	---	0	---	0	---	0	---	0	79	67
Melhania virescens	**---**	0	---	0	---	0	---	0	---	0	79	67
Striga bilabiata	**---**	0	---	0	---	0	---	0	---	0	79	67
Dicoma anomala	**---**	0	---	0	---	0	---	0	---	0	79	67
Eriocephalus luederitzianus	**---**	0	---	0	---	0	---	0	---	0	79	67
Brachiaria serrata	**---**	0	---	0	---	0	---	0	---	20	78	83
Scabiosa columbaria	**---**	0	---	0	---	0	---	0	---	10	72	67
Anginon streyi	**---**	0	---	0	---	0	---	0	---	0	67	50
Eragrostis nindensis	**---**	0	---	0	---	0	---	18	---	0	67	67
Tarchonanthus camphoratus	**---**	0	---	0	---	0	---	0	---	40	57	67
Rhynchosia totta	**---**	0	---	0	---	0	---	0	---	0	54	33
Hibiscus caesius	**---**	0	---	0	---	0	---	0	---	0	54	33
Kohautia aspera	**---**	0	---	0	---	0	---	0	---	0	54	33
Euphorbia spartaria	**---**	0	---	0	---	0	---	0	---	0	54	33
Lagarosiphon muscoides	**54**	75	45	67	---	0	---	0	---	0	---	0
Heteropogon contortus	**---**	0	---	0	---	0	---	0	49	80	68	100
Tragus racemosus	**---**	0	---	0	---	33	39	45	---	10	---	0
Dichrostachys cinerea	**---**	0	---	0	---	0	---	18	---	30	---	17
Schkuhria pinnata	**---**	0	---	0	---	0	---	0	38	40	---	33
Oxalis depressa	**---**	0	---	0	---	0	---	0	38	40	---	33
Aristida effusa	**---**	0	---	0	---	33	---	0	---	20	---	33
Tragus berteronianus	**---**	0	---	0	---	0	---	9	---	30	---	17
Kyllinga alba	**---**	0	---	0	---	0	---	18	---	30	---	0
Nidorella resedifolia	**---**	0	---	0	---	0	---	0	---	30	---	33
Eragrostis echinochloidea	**---**	0	---	0	---	33	---	0	---	10	---	33
Bulbostylis hispidula	**---**	0	---	0	---	0	---	27	---	0	---	17
Melinis repens subsp. *grandiflora*	**---**	0	---	0	---	0	---	9	---	20	---	17
Aristida adscensionis	**---**	0	---	0	---	0	---	18	---	20	---	0
Brachiaria nigropedata	**---**	0	---	0	---	0	---	0	---	30	---	17
Anthephora pubescens	**---**	0	---	0	---	0	---	0	---	30	---	17
Euclea undulata	**---**	0	---	0	---	0	---	0	---	30	---	17
Vachellia reficiens / luederitzii	**---**	25	---	0	---	0	---	0	---	10	---	17
Aristida rhiniochloa	**---**	0	---	0	---	33	---	0	---	10	---	17
Gisekia africana	**---**	0	---	0	---	0	---	18	---	0	---	17
Aristida meridionalis	**---**	0	---	0	---	0	---	18	---	0	---	17
Indigofera charlieriana	**---**	0	---	0	---	0	---	9	---	10	---	17
Tephrosia dregeana var. *dregeana*	**---**	0	---	0	---	0	---	9	---	20	---	0
Pogonarthria fleckii	**---**	0	---	0	---	0	---	18	---	0	---	17
Ziziphus mucronata	**---**	0	---	0	---	0	---	0	---	20	---	17
Monsonia glauca	**---**	0	---	0	---	0	---	0	---	20	---	17
Commelina livingstonii	**---**	0	---	0	---	0	---	0	---	20	---	17
Aristida congesta subsp. *congesta*	**---**	0	---	0	---	0	---	0	---	20	---	17
Thesium xerophyticum	**---**	0	---	0	---	0	---	0	---	10	---	33
Panicum coloratum	**---**	25	---	0	---	0	---	0	---	10	---	0
Vahlia capensis	**---**	0	---	33	---	0	---	9	---	0	---	0

Marsdenia macrantha and *Lagarosiphon muscoides*. A similar association has been described by Strohbach (2014a) in the eastern communal areas, south-east of the present study area. The absence of the hydrophytes *Nymphaea*, *Nymphoides* and *Echinochloa* indicates a shallow (considerably less than 1 m) and very temporary water habitat, which is not regularly flooded (Figures 5b, 6b). The few relevés were sampled at an altitude around 1190 m a.s.l.

2. Grasslands

Grasslands are limited in extent in Namibia and are often associated with wetland systems or desert environments. Within the study area, these are dominated by the plant families *Poaceae* (65 species), *Fabaceae* (22 species) and *Asteraceae* (21 species). Two higher order groupings could be recognised, but at this stage are not formally

described, pending an extensive revision of these grasslands in comparison to other similar types in Namibia, as well as in the South African Grassland Biome (Mucina and Rutherford 2006).

Overview of the grassland groupings:

2.1 Undefined upper hierarchy
- 2.1.1 *Ishana* grasslands (*Sporobolus*-dominated)
  - 2.1.1.1 *Sporobolus spicatus-Odyssea paucinervis* community
  - 2.1.1.2 *Aristido stipoidis-Willkommietum sarmentosae*
- 2.1.2 Mesic grasslands
  - 2.1.2.1 *Hilliardiello oligocephalae-Themedetum triandrae*
  - 2.1.2.2 *Geigerio otaviensis-Fingerhuthietum africanae*

2.1.1 Ishana grasslands (*Sporobolus*-dominated)

The *Sporobolus*-dominated grasslands are associated with pans and shallow water courses, typically the *ishana* and pans of the Cuvelai Delta (Le Roux et al. 1988; Clarke 1999; Mendelsohn et al. 2013) (*ishana*, plural, singular: *oshana*, vernacular for seasonally flooded shallow water courses in northern Namibia). The two associations described here resemble the Andoni grasslands as described by Le Roux et al. (1988), but distinct differences in species composition as well as height and density of the sward differentiate them from these.

2.1.1.1 Sporobolus spicatus-Odyssea paucinervis community

Number of relevés: 3
Number of species observed: 10
Estimated number of species: 13
Average species density in 1000 m^2: 6
Diagnostic species: ***Sporobolus spicatus, Leptochloa fusca, Odyssea paucinervis, Sporobolus acinifolius***
Constant species: *Dactyloctenium aegyptium*

Along the eastern fringe of the Omuramba Ovambo, on the farm Nukuwis, occurs an isolated clay pan. The pan is zoned in three concentric zones: The outer ring is a mixture of *Sporobolus spicatus*, with some *Odyssea paucinervis* and *Cynodon dactylon*, the following ring is dominated by *Leptochloa fusca*, whilst the inner ring is dominated by *Sporobolus acinifolius*. In the centre is a bare patch. The structure is best described as a low, open grassland (Figure 5c).

The soils consist of a heavy, whitish clay with 73% clay in the topsoil, increasing to 83% in the B-horizon. The pH ranged between 9.8 to 10.0, with the soil conductivity ranging between 4,700 to 6,480 µS/cm. Sodium content of the soils was 12,200 ppm. The high salinity is reflected in the presence of *Odyssea paucinervis* (Gibbs Russell et al. 1990; Müller 2007), but overall very low species richness. All stands grew at 1198 m a.s.l.

2.1.1.2 Aristido stipoidis-Willkommietum sarmentosae ass. nov.

Number of relevés: 11
Number of species observed: 67
Estimated number of species: 99
Average species density in 1000 m^2: 16
Type relevé: 2781 (holotypus), sampled on 2 April 2003 at 19.17861°S, 18.61083°E (Begus)
Hyphaene petersiana (t2) 0.1%, *Hyphaene petersiana* (s1) 1%, *Eragrostis trichophora* (gp) 10%, *Willkommia sarmentosa* (gp) 10%, *Sporobolus ioclados* (gp) 5%, *Odyssea paucinervis* (gp) 2%, *Microchloa caffra* (gp) 1%, *Aristida stipoides* (ga) 2%, *Eragrostis viscosa* (ga) 2%, *Chloris virgata* (ga) 1%, *Dactyloctenium aegyptium* (ga) 1%, *Pogonarthria fleckii* (ga) 1%, *Commelina erecta* (hl) 1%, *Hirpicium gazanioides* (hl) 1%, *Kyllinga alba* (hl) 1%, *Portulaca kermesina* (hl) 1%, *Sesuvium sesuvioides* (hl) 1%

Diagnostic species: ***Chloris virgata, Willkommia sarmentosa, Sporobolus ioclados, Aristida stipoides, Hirpicium gazanioides, Eragrostis viscosa, Dactyloctenium aegyptium,*** *Sesuvium sesuvioides*, *Ipomoea coptica*, *Cyperus atriceps*, *Commelina subulata*, *Blepharis leendertziae*, *Sericorema sericea*, *Eragrostis trichophora*, *Microchloa caffra*, *Xerophyta humilis*, *Ophioglossum lancifolium*

The *Aristido stipoidis-Willkommietum sarmentosae* form the matrix of the Omuramba Ovambo vegetation, being the typical short open grasslands of the '*Parkiesveld*' (Figures 5d, 6c). They are dominated by *Aristida stipoides*, *Sporobolus ioclados*, *Xerophyta humilis*, *Willkommia sarmentosa*, *Sporobolus acinifolius*, *Sericorema sericea* and *Eragrostis trichophora*. Embedded in this grassland are islands of *Terminalio prunioidis-Spirostachyetum africanae*, often associated with a central pan of the *Nymphoides indica-Echinochloa* community (Figure 7a). A similar landscape has also been described for the water course systems in the KAZA Transfrontier Conservation area, albeit with different species (Schaffer-Smith et al. 2022).

The A-horizon is about 10 cm deep and consists of a near-pure, white sand (94% sand and 5% clay), with a pH of 7.3 and an electric conductivity of 49 µS/cm. The B-horizon is slightly loamier with 7% clay and 92% sand and has a pH of 9.7. The steeply increased electric conductivity (1117 µS/cm) is due to sodium and calcium collecting in this horizon (1380 ppm Na and 1322 ppm Ca). The horizon has also a gleyic, mottled appearance. The *Aristido stipoidis-Willkommietum sarmentosae* occur at an altitudinal range of between 1164 and 1201 m a.s.l.

2.1.2 Mesic grasslands

The Mesic grasslands found within the Karstveld resemble the Grassland Biome in South Africa, in particular the Highveld Mesic Grasslands (Mucina and Rutherford 2006). As these grasslands contain several species which are not associated with the Grassland Biome, even restricted range endemics, two associations are recognized here.

2.1.2.1 Hilliardiello oligocephalae-Themedetum triandrae ass. nov.

Number of relevés: 10
Number of species observed: 115
Estimated number of species: 177
Average species density in 1000 m²: 30
Type relevé: 7953 (holotypus), sampled on 18 February 2008 at 19.63861°S, 17.77306°E (Neu Sommerau)
Heteropogon contortus (gp) 20%, *Brachiaria nigropedata* (gp) 10%, *Elionurus muticus* (gp) 10%, *Themeda triandra* (gp) 10%, *Anthephora pubescens* (gp) 5%, *Cymbopogon pospischilii* (gp) 2%, *Andropogon gayanus* (gp) 1%, *Brachiaria serrata* (gp) 1%, *Cymbopogon caesius* (gp) 1%, *Eragrostis lehmanniana* var. *lehmanniana* (gp) 1%, *Microchloa caffra* (gp) 0.5%, *Hilliardiella oligocephala* (hl) 2%, *Thesium xerophyticum* (hl) 2%, *Clematis villosa* subsp. *villosa* (hl) 1%, *Hypoxis iridifolia* (hl) 1%, *Ipomoea oblongata* (hl) 1%, *Scabiosa columbaria* (hl) 1%, *Chamaecrista mimosoides* (hl) 0.5%, *Corchorus asplenifolius* (hl) 0.5%, *Hermannia eenii* (hl) 0.5%, *Tephrosia dregeana* var. *dregeana* (hl) 0.5%

Diagnostic species: ***Themeda triandra, Eragrostis lehmanniana, Elionurus muticus, Hilliardiella oligocephala, Ipomoea oblongata, Hypoxis iridifolia, Eragrostis superba, Hermannia eenii, Hermannia depressa, Corchorus asplenifolius,*** *Wahlenbergia undulata*, *Solanum delagoense*, *Lantana angolensis*, *Hyparrhenia hirta*, *Hibiscus trionum*, *Convolvulus sagittatus*, *Pollichia campestris*, *Andropogon gayanus* var. *polycladus*, *Solanum lichtensteinii*, *Cymbopogon caesius*, *Urochloa oligotricha*, *Osteospermum muricatum*, *Listia heterophylla*, *Indigofera vicioides*, *Alternanthera pungens*, *Cynodon dactylon*, *Heteropogon contortus*, *Setaria pumila*, *Euphorbia inaequilatera*, *Urochloa brachyura*

The *Hilliardiello oligocephalae-Themedetum triandrae* forms a tall, closed grassland very similar to the Highveld Grasslands of the central and eastern Grassland Biome in South Africa (Mucina and Rutherford 2006) (Figures 5e, 6d). It is dominated by the grass species *Heteropogon contortus*, *Elionurus muticus*, *Cymbopogon caesius*, *Themeda triandra*, *Setaria pumila*, *Hyparrhenia hirta*, *Urochloa oligotricha* and *Cynodon dactylon*, whilst *Vachellia karroo* is the main encroaching species. As such, these grasslands are to be regarded as fire-climax grasslands. The regular occurrence of savanna and dryland species like *Andropogon gayanus*, *Hermannia eenii*, *Lantana angolensis* and *Thesium xerophyticum* (based on distribution data from GBIF 2022) differentiates this association from the South African Grassland Biome associations.

The *Hilliardiello oligocephalae-Themedetum triandrae* occur in intermontane valleys filled with deep red soils derived from phyllites of the Mulden Group. They occur at altitudes between 1460 and 1860 m a.s.l., on gently undulating, undulating and rolling slopes. No obvious stone cover has been observed. Next to bush encroachment and erosion, these grasslands are threatened by tillage for crop production. Most of the original vegetation in the Otavi valley has been transformed in this way; only in the Sommerau – Gauss valley north of Kombat pristine examples were found.

2.1.2.2 Geigerio otaviensis-Fingerhuthietum africanae ass. nov.

Number of relevés: 6
Number of species observed: 89
Estimated number of species: 140
Average species density in 1000 m²: 27
Type relevé: 7960 (holotypus), sampled on 19 February 2008 at 19.57389°S, 17.70111°E (Gauss)
Helichrysum cerastioides var. *aurosicum* (s2) 1%, *Amphiglossa triflora* (s2) 0.5%, *Eriocephalus luederitzianus* (s2) 0.5%, *Jamesbrittenia atropurpurea* subsp. *pubescens* (s2) 0.5%, *Tarchonanthus camphoratus* (s2) 0.5%, *Fingerhuthia africana* (gp) 20%, *Cymbopogon pospischilii* (gp) 10%, *Heteropogon contortus* (gp) 10%, *Brachiaria serrata* (gp) 5%, *Eragrostis nindensis* (gp) 1%, *Geigeria otaviensis* (hl) 1%, *Striga bilabiata* (hl) 1%, *Dicoma anomala* (hl) 0.5%, *Scabiosa columbaria* (hl) 0.5%, *Anginon streyi* (hl) 0.1

Diagnostic species: ***Fingerhuthia africana, Cymbopogon pospischilii, Striga bilabiata, Melhania virescens, Jamesbrittenia atropurpurea*** **subsp.** ***pubescens, Helichrysum cerastioides*** **var.** ***aurosicum, Geigeria otaviensis, Eriocephalus luederitzianus, Dicoma anomala, Brachiaria serrata, Scabiosa columbaria, Heteropogon contortus, Eragrostis nindensis, Anginon streyi,*** *Tarchonanthus camphoratus*, *Rhynchosia totta*, *Kohautia aspera*, *Hibiscus caesius*, *Euphorbia spartaria*

The *Geigerio otaviensis–Fingerhuthietum africanae* forms a short, moderately closed grassland dominated by *Heteropogon contortus*, *Cymbopogon pospischilii* and *Fingerhuthia africana* (Figures 5g, 6f). Conspicuous are also the dwarfshrubs *Jamesbrittenia atropurpurea* subsp. *pubescens*, *Helichrysum cerastioides* var. *aurosicum*, *Eriocephalus luederitzianus* and the restricted-range endemic *Geigeria otaviensis*. The occurrence of the savanna and dryland species *Fingerhuthia africana*, *Melhania virescens*, *Jamesbrittenia atropurpurea* subsp. *pubescens*, *Eriocephalus luederitzianus*, *Euphorbia spartaria* (based on distribution data from GBIF 2022) as well as the restricted-range endemic *Geigeria otaviensis* (Loots 2005) differentiate this association from similar associations in the Grassland Biome of South Africa. These grasslands occur on Auros shale bands as part of the Auros formation in the Abenab subgroup (Pickford 1995; Bechstädt et al. 2018), at an altitude of between 1950 and 1990 m a.s.l., on undulating to rolling slopes at the peak of the Otavi mountain range. The soils are extremely shallow, basically consisting of skeletal stone fragments of the Auros shale bands (Figure 6f). Although the extend of these grasslands is very limited, they are rather conspicuous on the mountain tops along the Otavi Valley (Figure 7b).

3. Thornbush savanna – Karst transition

The southern Karstveld vegetation transitions into the Thornbush savanna *sensu* Giess (1998) to the south, without a distinct 'border'. Many of the units found are strongly influenced by shallow subsurfacing rock formations of the Otavi group, thus the very strong relations to the Karstveld

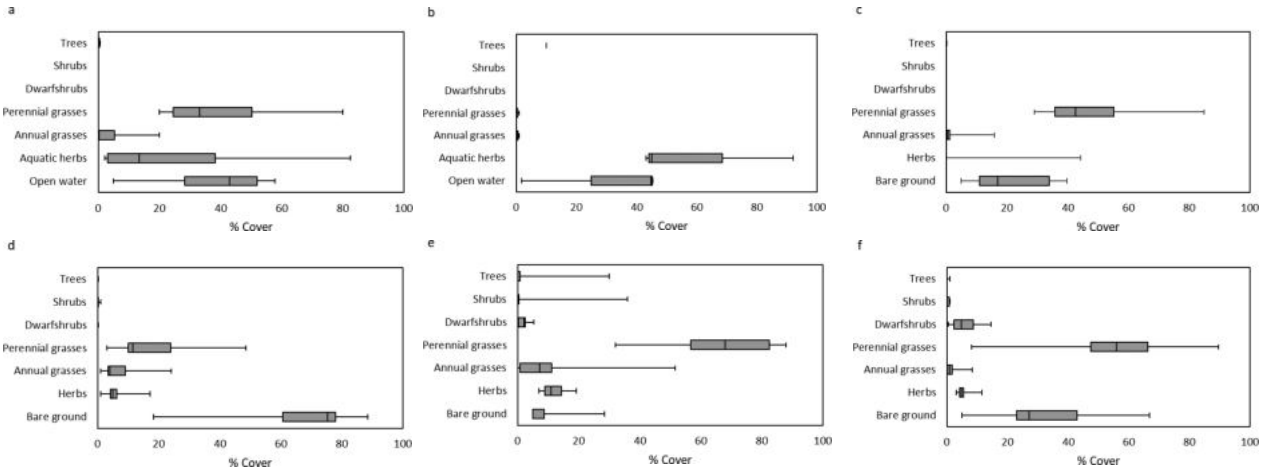

Figure 5. Typical structure of the associations of the wet- and grasslands: (**a**) *Nymphoides indica–Echinochloa pyramidalis* community; (**b**) *Panicum gilvum–Marsilea nubica* community; (**c**) *Sporobolus spicatus–Odyssea paucinervis* community; (**d**) *Aristido stipoidis-Willkommietum sarmentosae*; (**e**) *Hilliardiello oligocephalae-Themedetum triandrae*; (**f**) *Geigerio otaviensis-Fingerhuthietum africanae*.

Figure 6. Typical views of the associations of the wet- and grasslands: (**a**) Example of the *Nymphoides indica-Echinochloa pyramidalis* community, relevé 4097, ca 50 km east of the study area; (**b**) *Panicum gilvum-Marsilea nubica* community, relevé 7776; (**c**) *Aristido stipoidis-Willkommietum sarmentosae*, relevé 7773, foreground. In the background is a *Terminalio prunioidis-Spirostachyetum africanae* island; (**d**) *Hilliardiello oligocephalae-Themedetum triandrae*, relevé 7947; (**e**) *Geigerio otaviensis-Fingerhuthietum africanae*, relevé 7960; (**f**) soil surface of the *Geigerio otaviensis-Fingerhuthietum africanae* habitat at relevé 7960.

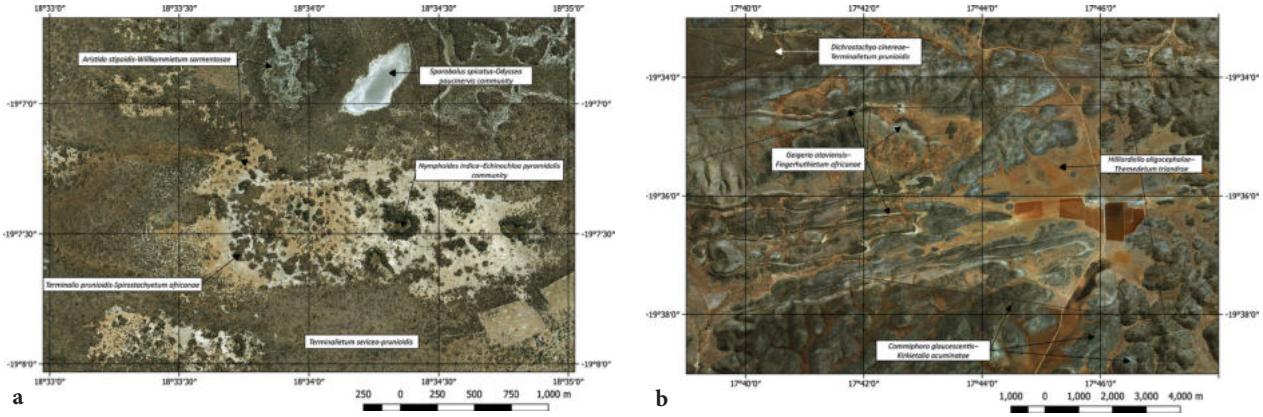

Figure 7. a Aerial image showing the mosaic of vegetation associations. (**a**) A portion of the Omuramba Ovambo at the farm Nukuwis. Alternatively to the *Terminalietum sericeo-prunioidis*, the *Combreto apiculati-Terminalietum prunioidis* can surround this mosaic, depending on the depth of the Kalahari sand cover. (**b**) The central Otavi mountains north of Kombat. The mountains are covered by one of the three associations of the *Commiphoro glaucescentis-Kirkietalia acuminatae*, depending on steepness and massiveness of the rocks, whilst the light-coloured bands on top of the mountains represent the Auros shales with a cover of *Geigerio otaviensis-Fingerhuthietum africanae*. Image source: Microsoft Maps (Bing Maps).

Proper types. Within this study area, the thornbush savanna is dominated by the families *Poaceae* (105 species), *Fabaceae* (74 species) and *Asteraceae* (48 species). Four associations were identified within the study area belonging to this class; these are however not assigned to any orders or alliances pending further revision of the Thornbush savanna types. An abbreviated synoptic table is presented in Table 3, whilst the full synoptic table is available in Suppl. material 3.

Overview of the Thornbush savannah – Karst transition syntaxa:

3.1 Undefined upper hierarchy
- 3.1.1.1 *Combreto hereroense-Tarchonanthoetum camphorate*
- 3.1.1.2 *Aristido pilgeri-Vachellietum eriolobae*
- 3.1.1.3 *Cenchro ciliaris-Senegalietum detinentis*
  - 3.1.1.3.1 *Cenchro ciliaris-Senegalietum detinentis typicum*
  - 3.1.1.3.2 *Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae*
- 3.1.1.4 *Eucleo undulatae-Oleetum africanae*

3.1.1.1 Combreto hereroense-Tarchonanthoetum camphorati ass. nov.

Number of relevés: 93
Number of species observed: 226
Estimated number of species: 368
Average species density in 1000 m^2: 48
Type relevé: 4318 (holotypus), sampled on 19 March 1997 at 19.69361°S, 18.05528°E (John Pandeni Research Station / Gressenhof)

Combretum hereroense (s1) 5%, *Tarchonanthus camphoratus* (s1) 5%, *Senegalia mellifera* subp. *detinens* (s1) 2%, *Senegalia cinerea* (s1) 0.1%, *Ziziphus mucronata* (s1) 0.1%, *Grewia flava* (s2) 1%, *Dichrostachys cinerea* (s2) 0.3%, *Euclea undulata* (s2) 0.3%, *Ozoroa paniculosa* (s2) 0.3%, *Searsia ciliata* (s2) 0.3%, *Grewia bicolor* (s2) 0.1%, *Lantana angolensis* (s2) 0.1%, *Anthephora pubescens* (gp) 1%, *Aristida congesta* subsp. *congesta* (gp) 1%, *Brachiaria nigropedata* (gp) 1%, *Schmidtia pappophoroides* (gp) 1%, *Andropogon gayanus* (gp) 0.3%, *Cymbopogon pospischilii* (gp) 0.3%, *Fingerhuthia africana* (gp) 0.3%, *Heteropogon contortus* (gp) 0.3%, *Panicum coloratum* (gp) 0.3%, *Pogonarthria squarrosa* (gp) 0.3%, *Stipagrostis uniplumis* var. *uniplumis* (gp) 0.3%, *Aristida rhiniochloa* (ga) 60%, *Pogonarthria fleckii* (ga) 2%, *Urochloa brachyura* (ga) 1%, *Aristida adscensionis* (ga) 0.3%, *Aristida effusa* (ga) 0.3%, *Aristida stipoides* (ga) 0.3%, *Tragus berteronianus* (ga) 0.3%, *Tragus racemosus* (ga) 0.3%, *Triraphis purpurea* (ga) 0.3%, *Eustachys paspaloides* (ga) 0.1%, *Indigofera charlieriana* (hl) 1%, *Bulbostylis hispidula* (hl) 0.3%, *Cyperus palmatus* (hl) 0.3%, *Dicoma anomala* (hl) 0.3%, *Hermannia tomentosa* (hl) 0.3%, *Indigofera pechuelii* (hl) 0.3%, *Kyphocarpa angustifolia* (hl) 0.3%, *Limeum sulcatum* (hl) 0.3%, *Melhania virescens* (hl) 0.3%, *Otoptera burchellii* (hl) 0.3%, *Rotheca myricoides* (hl) 0.3%, *Seddera suffruticosa* (hl) 0.3%, *Sesamum triphyllum* (hl) 0.3%, *Acalypha segetalis* (hl) 0.1%, *Aptosimum decumbens* (hl) 0.1%, *Euphorbia inaequilatera* (hl) 0.1%, *Geigeria ornativa* (hl) 0.1%, *Hibiscus caesius* (hl) 0.1%, *Pentarrhinum insipidum* (hl) 0.1%, *Trochomeria macrocarpa* subsp. *vitifolia* (hl) 0.1%

Diagnostic species: *Brachiaria nigropedata*, *Anthephora pubescens*, *Sesamum triphyllum*, *Rotheca myricoides*, *Schmidtia pappophoroides*, *Vernonia fastigiata*, *Dicoma anomala*, *Ozoroa paniculosa*, *Tragus racemosus*, *Triraphis purpurea*, *Indigofera charlieriana*, *Indigofera pechuelii*

Constant species: ***Senegalia mellifera* subsp. *detinens*, *Tarchonanthus camphoratus*, *Combretum hereroense*, *Heteropogon contortus*,** *Dichrostachys cinerea*, *Stipagrostis uniplumis* var. *uniplumis*, *Fingerhuthia africana*, *Grewia flava*, *Seddera suffruticosa*, *Melinis repens* subsp. *grandiflora*, *Combretum imberbe*, *Eragrostis trichophora*, *Aristida rhiniochloa*, *Urochloa brachyura*, *Melhania virescens*, *Euclea undulata*, *Enneapogon scoparius*

The *Combreto hereroense-Tarchonanthoetum camphorati* forms an extensive low bushland to tall shrubland south of Grootfontein towards the Omuramba Omatako (Figures 8a, 9a). These bushlands are dominated by the

Table 3. Abbreviated synoptic table for the Thornbush savanna - Karstveld transition, showing all species occurring in more than 10% of relevés of this group, with fidelity (phi coefficient × 100) and frequency of occurrence (%).

Association	**3.1.1.1**		**3.1.1.2**		**3.1.1.3**				**3.1.1.4**	
Subassociation					**3.1.1.3.1**		**3.1.1.3.2**			
No of relevés	**93**		**56**		**71**		**145**		**32**	
Species	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**
Brachiaria nigropedata	59	54	---	5	---	0	---	1	---	6
Anthephora pubescens	53	87	---	7	---	1	---	23	27	63
Sesamum triphyllum	51	45	---	2	---	0	---	3	---	9
Rotheca myricoides	51	39	---	0	---	0	---	1	---	6
Schmidtia pappophoroides	49	78	---	34	---	7	---	23	---	19
Vernonia fastigiata	48	37	---	4	---	3	---	2	---	0
Dicoma anomala	46	38	---	2	---	0	---	1	---	9
Ozoroa paniculosa	43	68	---	34	---	3	---	17	---	22
Tragus racemosus	43	68	---	4	---	7	---	19	20	47
Triraphis purpurea	42	37	---	2	---	4	---	7	---	3
Indigofera charlieriana	42	66	---	4	---	7	---	20	18	44
Indigofera pechuelii	40	20	---	0	---	0	---	1	---	0
Hermannia eenii	---	5	58	54	---	6	---	3	---	0
Aristida pilgeri	---	5	55	43	---	0	---	1	---	0
Melhania acuminata	---	2	55	54	---	4	---	11	---	3
Vachellia erioloba	---	6	49	57	---	14	---	12	---	3
Terminalia sericea	---	0	49	30	---	0	---	1	---	0
Senegalia cinerea	---	4	47	59	---	20	---	12	---	9
Dicoma schinzii	---	15	45	45	---	1	---	5	---	3
Waltheria indica	---	9	43	50	---	4	---	17	---	6
Digitaria seriata	---	0	41	29	---	1	---	3	---	3
Heliotropium nelsonii	---	3	---	0	52	48	---	11	---	3
Leucosphaera bainesii	---	2	---	0	52	45	---	12	---	0
Monechma genistifolium	---	0	---	0	51	37	---	5	---	0
Ipomoea obscura var. *obscura*	---	1	---	2	49	35	---	3	---	0
Asparagus cooperi	---	0	---	0	46	30	---	4	---	0
Eragrostis porosa	---	4	---	2	43	48	---	14	---	13
Solanum tettense var. *renschii*	---	0	---	2	43	34	---	7	---	3
Hibiscus calyphyllus	---	0	---	2	42	35	---	10	---	3
Geigeria acaulis	---	0	---	2	41	23	---	0	---	0
Boscia albitrunca	---	0	---	9	41	48	---	16	---	13
Hibiscus palmatus	---	0	---	0	41	23	---	2	---	0
Ptycholobium biflorum subsp. *angolensis*	---	3	---	0	40	42	---	19	---	6
Corchorus tridens	---	3	---	0	63	58	---	9	---	0
Olea europaea subsp. *africana*	---	0	---	0	---	0	---	0	100	100
Fingerhuthia africana	30	74	---	4	---	7	---	47	46	91
Digitaria eriantha	---	1	---	0	---	0	---	5	45	31
Euclea undulata	21	62	---	21	---	3	---	39	43	84
Croton gratissimus	---	3	---	7	---	14	22	46	41	63
Kohautia aspera	---	10	---	4	---	0	---	8	40	38
Heteropogon contortus	28	81	---	27	---	8	---	59	38	91
Senegalia mellifera subsp. *detinens*	---	88	---	89	---	87	9	97	---	97
Dichrostachys cinerea	---	77	13	88	---	77	---	76	---	66
Grewia flava	---	73	---	61	---	73	---	76	---	66
Combretum hereroense	24	85	---	55	---	10	18	79	20	81
Vachellia reficiens / luederitzii	---	29	---	68	21	87	---	69	21	88
Eragrostis trichophora	---	68	---	45	21	80	---	52	---	56
Tarchonanthus camphoratus	30	85	---	21	---	39	---	63	---	66
Stipagrostis uniplumis var. *uniplumis*	17	75	22	80	---	42	---	50	---	47
Melhania virescens	---	65	---	7	---	48	15	70	32	88
Lantana angolensis	---	59	---	41	---	51	---	59	---	69
Urochloa brachyura	16	67	---	50	---	45	---	50	---	41
Seddera suffruticosa	21	71	---	16	---	41	---	57	---	66
Ziziphus mucronata	---	51	---	59	---	39	---	50	18	72
Melinis repens subsp. *grandiflora*	23	70	---	21	---	52	---	47	---	44
Enneapogon scoparius	17	61	---	5	---	24	16	60	28	72
Otoptera burchellii	16	60	---	23	14	58	---	43	---	38
Eragrostis echinochloidea	---	25	---	9	---	51	20	66	33	78
Cenchrus ciliaris	---	23	---	4	29	75	12	57	24	69
Searsia marlothii	10	56	---	21	---	10	11	57	39	84
Combretum imberbe	31	69	---	39	---	6	---	41	---	38

Association	3.1.1.1		3.1.1.2		3.1.1.3				3.1.1.4	
Subassociation					3.1.1.3.1		3.1.1.3.2			
No of relevés	93		56		71		145		32	
Species	phi	%	phi	%	phi	%	phi	%	phi	%
Aristida rhiniochloa	32	68	---	21	---	27	---	37	---	31
Peltophorum africanum	18	56	14	52	---	3	---	34	---	47
Enneapogon cenchroides	---	42	---	7	22	56	---	36	---	38
Aristida effusa	---	41	---	9	---	45	12	44	---	25
Grewia flavescens	---	9	---	45	11	49	4	42	---	47
Ocimum americanum var. *americanum*	---	40	---	41	---	32	---	35	---	25
Hibiscus caesius	---	32	---	11	---	7	14	45	36	66
Aptosimum decumbens	---	37	---	29	---	28	---	30	---	28
Ehretia rigida	---	10	---	11	33	59	9	37	---	28
Pogonarthria fleckii	24	52	---	27	---	37	---	17	---	16
Sericorema sericea	24	51	---	4	---	10	---	30	23	50
Phyllanthus maderaspatensis	---	29	---	18	---	31	---	31	---	31
Terminalia prunioides	---	12	---	21	---	14	28	49	---	28
Aristida adscensionis	21	45	---	9	---	37	---	22	---	19
Aristida congesta subsp. *congesta*	24	48	12	38	---	32	---	11	---	6
Urochloa oligotricha	9	37	---	4	---	27	---	23	27	53
Evolvulus alsinoides	---	12	21	48	18	45	---	21	---	19
Tragus berteronianus	---	31	---	4	20	42	---	22	---	25
Eragrostis nindensis	15	33	---	2	---	10	15	34	---	28
Grewia bicolor	---	11	---	21	28	45	---	26	---	6
Limeum sulcatum	24	45	---	5	---	8	---	17	26	47
Tephrosia dregeana var. *dregeana*	---	27	---	29	---	8	---	22	---	31
Ocimum filamentosum	---	6	---	5	21	38	14	32	---	22
Pavonia burchellii	---	12	---	23	12	34	---	21	---	28
Geigeria ornativa	---	8	---	29	---	28	---	26	---	16
Commiphora glandulosa	---	22	---	18	---	0	18	33	---	22
Nidorella resedifolia	---	8	---	13	22	38	9	27	---	16
Gymnosporia senegalensis	---	6	---	16	---	7	12	33	36	53
Stipagrostis hirtigluma subsp. *hirtigluma*	---	1	---	2	---	20	33	41	---	19
Clerodendrum ternatum	---	4	---	18	13	30	12	28	---	16
Rhynchosia totta	---	16	---	14	---	15	9	26	---	25
Searsia ciliata	32	44	---	13	---	10	---	13	---	16
Enneapogon desvauxii	---	13	---	0	---	11	8	28	40	53
Kyphocarpa angustifolia	16	33	15	32	---	24	---	6	---	6
Commelina livingstonii	39	49	---	4	---	10	---	10	---	22
Catophractes alexandri	---	9	---	5	---	17	20	31	---	19
Leucas pechuelii	---	4	---	2	38	44	11	24	---	6
Phyllanthus pentandrus	---	8	---	11	---	21	5	23	19	34
Heliotropium ovalifolium	---	9	---	14	---	6	3	23	37	50
Panicum coloratum	36	45	---	5	---	6	---	8	---	25
Eragrostis rigidior	---	5	26	39	14	30	---	13	---	6
Melinis repens subsp. *repens*	---	23	20	34	---	11	---	11	---	13
Eriocephalus luederitzianus	14	26	---	0	---	14	---	19	---	19
Commiphora angolensis	---	6	---	5	---	23	13	24	---	16
Chascanum pinnatifidum	---	12	---	4	31	35	---	19	---	0
Acalypha segetalis	31	39	---	0	---	3	---	12	---	25
Commiphora africana	---	15	---	0	---	10	11	23	18	28
Pupalia lappacea	---	9	---	5	23	34	---	14	---	22
Combretum apiculatum	12	26	---	11	---	0	---	15	20	31
Rhynchosia minima	10	24	---	2	---	11	---	15	17	28
Pogonarthria squarrosa	20	30	35	41	---	1	---	6	---	0
Eragrostis superba	37	41	---	2	---	3	---	10	---	19
Hermannia tomentosa	26	33	---	13	---	8	---	10	---	9
Cymbopogon pospischilii	39	44	---	4	---	1	---	6	---	25
Helinus spartioides	19	26	---	5	---	11	---	14	---	9
Raphionacme lanceolata	---	12	---	2	---	21	---	18	---	13
Acrotome inflata	---	17	---	5	22	31	---	7	---	16
Solanum lichtensteinii	12	23	---	2	18	27	---	7	---	13
Aristida stipoides	35	37	---	0	---	3	---	8	---	19
Sida ovata	---	4	25	32	---	13	---	13	---	9
Andropogon gayanus var. *polycladus*	32	35	---	7	---	0	---	6	---	19
Eragrostis lehmanniana	---	2	31	34	---	0	10	19	---	9
Gisekia africana	26	31	---	7	---	3	---	7	---	19
Andropogon chinensis	30	32	---	2	---	3	---	7	---	19

Association	3.1.1.1		3.1.1.2		3.1.1.3				3.1.1.4	
Subassociation					3.1.1.3.1		3.1.1.3.2			
No of relevés	93		56		71		145		32	
Species	phi	%	phi	%	phi	%	phi	%	phi	%
Brachiaria deflexa	---	6	---	0	19	25	---	12	---	19
Albizia anthelmintica	---	2	---	5	31	30	---	15	---	0
Bothriochloa radicans	---	5	---	2	---	11	24	22	---	3
Mundulea sericea	---	5	---	2	---	1	12	20	30	31
Commiphora pyracanthoides	---	0	---	2	37	34	---	13	---	6
Pentarrhinum insipidum	8	19	---	5	---	3	---	8	30	34
Hyphaene petersiana	---	13	27	27	---	1	---	11	---	0
Oxygonum alatum	---	12	---	7	14	21	---	7	---	13
Commelina benghalensis	---	2	---	5	34	34	---	8	---	9
Ruellia species	---	1	---	0	30	27	11	16	---	3
Aizoon virgatum	---	0	---	0	32	30	---	14	---	6
Monechma spartioides	---	0	27	30	---	6	---	12	---	16
Hermannia modesta	---	11	---	2	24	27	---	6	---	13
Sporobolus panicoides	---	4	---	4	---	4	8	17	26	28
Philenoptera nelsii	---	0	23	27	27	30	---	4	---	0
Cyperus palmatus	26	27	---	0	---	11	---	3	---	13
Brachiaria malacodes	11	16	---	0	---	14	---	9	---	9
Indigofera daleoides	36	31	---	14	---	1	---	2	---	0
Kohautia caespitosa subsp. *brachyloba*	11	17	---	2	22	24	---	3	---	6
Vachellia hebeclada subsp. *hebeclada*	---	5	---	13	31	30	---	5	---	0
Euphorbia inaequilatera	---	9	---	0	21	24	---	7	---	16
Ruelliopsis damarensis	---	11	---	4	---	15	---	9	---	13
Talinum arnotii	---	3	---	7	39	32	---	6	---	0
Sporobolus fimbriatus	---	2	16	20	---	8	---	11	---	9
Tinnea rhodesiana	19	16	---	0	---	0	15	14	---	3
Senegalia hereroensis	15	22	---	0	---	1	---	4	31	31
Ipomoea bolusiana	---	4	---	16	---	7	---	12	---	3
Peliostomum leucorrhizum	---	1	---	0	35	27	---	12	---	0
Hermannia quartiniana	---	5	---	13	---	6	---	10	---	16
Aristida meridionalis	31	26	---	14	---	0	---	2	---	0
Pechuel-Loeschea leubnitziae	---	5	---	11	11	15	---	8	---	6
Antiphiona pinnatisecta	12	17	---	5	---	0	---	6	20	22
Monechma divaricatum	---	1	---	5	---	7	21	17	---	3
Achyranthes aspera var. *sicula*	---	8	---	0	13	17	---	7	---	16
Dicoma tomentosa	---	3	---	9	15	18	---	7	---	9
Solanum delagoense	---	3	---	5	---	8	15	14	---	3
Ipomoea sinensis	---	5	---	0	30	23	---	8	---	0
Tribulus terrestris	---	1	---	0	25	20	---	11	---	3
Bidens biternata	---	6	---	2	---	6	---	8	34	31
Bulbostylis hispidula	10	14	---	7	---	11	---	3	---	6
Hermbstaedtia odorata	22	19	---	4	---	4	---	5	---	6
Helinus integrifolius	---	8	---	0	26	21	---	6	---	3
Hypoestes forskaolii	---	0	---	0	---	7	14	15	---	16
Setaria verticillata	---	8	---	0	11	14	---	7	---	13
Chloris virgata	---	9	---	0	26	20	---	6	---	0
Petalidium englerianum	---	2	---	0	---	6	20	15	---	6
Aloe zebrina	9	13	---	13	---	0	---	6	---	9

phanerophytes *Tarchonanthus camphoratus*, *Senegalia mellifera* subsp. *detinens*, *Combretum hereroense*, *Euclea undulata*, *Dichrostachys cinerea*, *Croton gratissimus*, *Combretum imberbe*, *Combretum apiculatum* and *Catophractes alexandri*. The grass layer is dominated by *Aristida rhiniochloa*, *Stipagrostis uniplumis* var. *uniplumis*, *Schmidtia pappophoroides*, *Enneapogon scoparius*, *Aristida adscensionis*, *Pogonarthria fleckii*, *Urochloa oligotricha*, *Trachypogon spicatus*, *Fingerhuthia africana* and *Aristida congesta* subsp. *congesta*. *Schmidtia pappophoroides*, *Brachiaria nigropedata*, *Fingerhuthia africana* and *Anthephora pubescens* form the palatable climax grasses of this association.

This association occurs on shallow to moderately deep, medium-textured soils (often Leptsols) over calcrete, as part of lower Kalahari deposits (Coetzee et al. 1998). These are underlain by the ancient Grootfontein Metamorphic Complex (Geological Survey 1980; South African Committee for Stratigraphy 1980; Kamona and Günzel 2007). The calcrete is often evident as gravel (up to 40%) on the surface, with occasional small, medium and large calcrete stones visible on the surface. Although the topography is generally flat with less than 2° slope, the altitude ranges between 1170 and 1850 m a.s.l.

3.1.1.2 Aristido pilgeri-Vachellietum eriolobae ass. nov.

Number of relevés: 55
Number of species observed: 155
Estimated number of species: 292
Average species density in 1000 m²: 32
Type relevé: 7803 (holotypus), sampled on 26 April 2007 at 19.93222°S, 17.96028°E (Omambonde Tal)
Vachellia erioloba (t2) 10%, *Vachellia luederitzii* (t3) 2%, *Philenoptera nelsii* (t3) 1%, *Senegalia mellifera* subsp. *mellifera* (s1) 20%, *Dichrostachys cinerea* (s1) 5%, *Grewia flava* (s1) 5%, *Senegalia cinerea* (s1) 5%, *Grewia bicolor* (s1) 2%, *Grewia flavescens* (s1) 2%, *Combretum hereroense* (s1) 1%, *Ehretia rigida* (s1) 0.4%, *Tarchonanthus camphoratus* (s1) 0.4%, *Pechuel-Loeschea leubnitziae* (s2) 1%, *Asparagus nelsii* (s2) 0.4%, *Commiphora angolensis* (s2) 0.4%, *Lantana angolensis* (s2) 0.4%, *Stipagrostis uniplumis* var. *uniplumis* (gp) 40%, *Aristida pilgeri* (gp) 5%, *Eragrostis rigidior* (gp) 5%, *Pogonarthria squarrosa* (gp) 0.4%, *Melinis repens* subsp. *grandiflora* (ga) 1%, *Urochloa brachyura* (ga) 0.4%, *Hermannia eenii* (hl) 5%, *Aptosimum angustifolium* (hl) 1%, *Hibiscus caesius* (hl) 0.4%, *Kyphocarpa angustifolia* (hl) 0.4%, *Melhania acuminata* (hl) 0.4%, *Nidorella resedifolia* (hl) 0.4%, *Otoptera burchellii* (hl) 0.4%, *Phyllanthus pentandrus* (hl) 0.4%, *Polydora steetziana* (hl) 0.4%, *Rhynchosia totta* (hl) 0.4%, *Seddera suffruticosa* (hl) 0.4%, *Waltheria indica* (hl) 0.4%

Diagnostic species: *Hermannia eenii*, *Aristida pilgeri*, *Melhania acuminata*, *Vachellia erioloba*, *Terminalia sericea*, *Senegalia cinerea*, *Dicoma schinzii*, *Waltheria indica*, *Digitaria seriata*

Constant species: ***Senegalia mellifera* subsp. *detinens*, *Dichrostachys cinerea,*** *Stipagrostis uniplumis* var. *uniplumis*, *Vachellia reficiens / luederitzii*, *Grewia flava*

The *Aristido pilgeri-Vachellietum eriolobae* is mainly found near riverine systems through sandy substrate. Typical is the floodplain valley of the Omambonde Omatako along the southern edge of the study area, but also the Ugab headwaters south-west of Otavi and to the north and east of the Omuramba Ovambo between Maroelaboom and Oshivelo. The structure is typically a moderately closed tall bushland dominated by *Senegalia mellifera* subsp. *detinens*, *Terminalia sericea*, *Peltophorum africanum*, *Vachellia erioloba*, *Senegalia cinerea*, *Dichrostachys cinerea*, *Vachellia reficiens / luederitzii* and *Philenoptera nelsii*. In the grass layer, *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis trichophora*, *Eragrostis rigidior*, *Eragrostis rotifer*, *Eragrostis lehmanniana*, *Aristida congesta* subsp. *congesta*, *Schmidtia pappophoroides* and *Pogonarthria fleckii* dominate (Figures 8b, 9b).

Strohbach (2002) described an *Acacia erioloba-Stipagrostis uniplumis* association which resembles the *Aristido pilgeri-Vachellietum eriolobae*. According to her, the soils are generally loamy sands or occasionally sandy loams overlying the Omingonde formation. The topography is generally flat (< 2° slope), on altitudes between 1200 and 1500 m a.s.l. The *Aristido pilgeri-Vachellietum eriolobae* is related to the *Schmidtio kalahariensis-Vachellietum eriolobae* described by Strohbach (2021; see also Strohbach et al. 2019) as well as to the Stella Bushveld and the Kimberly Thornveld in the Savanna Biome of South Africa (Mucina and Rutherford 2006). Yet the species composition is distinctly different from these.

3.1.1.3 Cenchro ciliaris-Senegalietum detinentis ass. nov.

Number of relevés: 216
Number of species observed: 323
Estimated number of species: 490
Average species density in 1000 m²: 44
Type relevé: 3330 (holotypus), sampled on 14 March 2002 at 19.85778°S, 17.42083°E (Okoruso)
Senegalia mellifera subsp. *detinens* (s1) 5%, *Vachellia reficiens* (s1) 5%, *Ziziphus mucronata* (s1) 0.5%, *Lycium bosciifolium* (s1) 0.2%, *Grewia flava* (s1) 0.1%, *Pechuel-Loeschea leubnitziae* (s2) 0.5%, *Hibiscus calyphyllus* (s2) 0.2%, *Ziziphus mucronata* (s2) 0.2%, *Aizoon virgatum* (s2) 0.1%, *Asparagus cooperi* (s2) 0.1%, *Ehretia rigida* (s2) 0.1%, *Heliotropium nelsonii* (s2) 0.1%, *Leucosphaera bainesii* (s2) 0.1%, *Ptycholobium biflorum* (s2) 0.1%, *Solanum lichtensteinii* (s2) 0.1%, *Tarchonanthus camphoratus* (s2) 0.1%, *Eragrostis trichophora* (gp) 25%, *Cenchrus ciliaris* (gp) 20%, *Eragrostis echinochloidea* (gp) 1%, *Eragrostis rotifer* (gp) 0.1%, *Urochloa oligotricha* (ga) 5%, *Aristida adscensionis* (ga) 0.1%, *Aristida effusa* (ga) 0.1%, *Eragrostis porosa* (ga) 0.1%, *Melinis repens* subsp. *grandiflora* (ga) 0.1%, *Tragus berteronianus* (ga) 0.1%, *Nidorella resedifolia* (hl) 0.5%, *Cucumis anguria* (hl) 0.2%, *Ocimum filamentosum* (hl) 0.2%, *Commicarpus pentandrus* (hl) 0.1%, *Corchorus tridens* (hl) 0.1%, *Gomphrena celosioides* (hl) 0.1%, *Hibiscus palmatus* (hl) 0.1%, *Indigastrum costatum* (hl) 0.1%, *Ipomoea obscura* var. *obscura* (hl) 0.1%, *Ipomoea sinensis* (hl) 0.1%, *Ocimum americanum* var. *americanum* (hl) 0.1%, *Osteospermum muricatum* subsp. *muricatum* (hl) 0.1%, *Phyllanthus maderaspatensis* (hl) 0.1%, *Rhynchosia minima* (hl) 0.1%, *Ruellia* species (hl) 0.1%, *Senna italica* (hl) 0.1%, *Tribulus terrestris* (hl) 0.1%

Diagnostic species: *Corchorus tridens*

Constant species: ***Senegalia mellifera* subsp. *detinens,*** *Dichrostachys cinerea*, *Vachellia reficiens / luederitzii*, *Grewia flava*, *Melhania virescens*, *Cenchrus ciliaris*, *Eragrostis trichophora*, *Eragrostis echinochloidea*

The *Cenchro ciliaris-Senegalietum detinentis* forms the relatively dense bushlands south of the Otavi Mountain range, roughly covering the triangle Rietfontein – Otavi – Otjiwarongo. The association occurs on the flat to undulating landscapes formed by the marbles and schists of the Swakop Group (Geological Survey 1980; South African Committee for Stratigraphy 1980; Schneider 2004; Kamona and Günzel 2007). While Strohbach (2002) recognised two separate communities (*Acacia mellifera - Cenchrus ciliaris* community and the *Acacia mellifera - Stipagrostis hirtigluma* community, respectively), due to their very similar composition and structure, these are recognised here as subassociations of the *Cenchro ciliaris-Senegalietum detinentis*.

3.1.1.3.1 Cenchro ciliaris-Senegalietum detinentis typicum subass. nov.

Number of relevés: 71
Number of species observed: 216
Estimated number of species: 324
Average species density in 1000 m^2: 46
Diagnostic species: ***Corchorus tridens,*** *Heliotropium nelsonii*, *Leucosphaera bainesii*, *Monechma genistifolium*, *Ipomoea obscura* var. *obscura*, *Asparagus cooperi*, *Eragrostis porosa*, *Solanum tettense* var. *renschii*, *Hibiscus calyphyllus*, *Geigeria acaulis*, *Boscia albitrunca*, *Hibiscus palmatus*, *Ptycholobium biflorum* subsp. *angolensis*
Constant species: ***Vachellia reficiens / luederitzii, Senegalia mellifera* subsp. *detinens,*** *Eragrostis trichophora*, *Dichrostachys cinerea*, *Cenchrus ciliaris*, *Grewia flava*

Strohbach (2002) described this subassociation as her *Acacia mellifera - Cenchrus cilliaris* association. Typically, the *Cenchro ciliaris-Senegalietum detinentis typicum* forms a moderately closed tall shrubland or short bushland, depending on the density of trees in the stand (Figures 8c, 9c). The vegetation is described by Strohbach (2002) as less encroached with a more prominent perennial grass sward than the *Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae.* The phanerophytic layer is dominated by *Senegalia mellifera* subsp. *detinens*, *Vachellia reficiens / luederitzii*, *Dichrostachys cinerea* and *Grewia* species, with occasionally also *Philenoptera nelsii*, *Vachellia tortilis* subsp. *heteracantha*, *Tarchonanthus camphoratus* and *Croton gratissimus* also occurring. The grass sward is dominated by *Eragrostis trichophora*, *Cenchrus ciliaris*, *Eragrostis rigidior*, *Eragrostis porosa*, *Enneapogon cenchroides*, *Stipagrostis uniplumis* var. *uniplumis* and *Sporobolus fimbriatus.*

The *Cenchro ciliaris-Senegalietum detinentis typicum* occurs on deeper sandy loams and sandy clay loams, mostly Chromic Cambisols. There has only limited stone cover recorded on single relevés. The subassociation occurs on flat to gently undulating slopes at an altitudinal range of between 1170 and 1550 m a.s.l.

3.1.1.3.2 Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae subass. nov.

Number of relevés: 145
Number of species observed: 254
Estimated number of species: 431
Average species density in 1000 m^2: 43
Type relevé: 3521 (holotypus), sampled on 25 April 2002 at 20.05667°S, 17.04750°E (Gerhardtshausen / Felsenquelle)
Peltophorum africanum (t3) 5%, *Senegalia mellifera* subsp. *detinens* (s1) 40%, *Croton gratissimus* var. *gratissimus* (s1) 10%, *Dichrostachys cinerea* (s1) 5%, *Vachellia reficiens* (s1) 5%, *Grewia flava* (s1) 2%, *Tarchonanthus camphoratus* (s1) 2%, *Terminalia prunioides* (s1) 2%, *Catophractes alexandri* (s1) 1%, *Combretum hereroense* (s1) 0.5%, *Euclea undulata* (s1) 0.5%, *Searsia marlothii* (s1) 0.2%, *Ehretia rigida* (s2) 0.5%, *Hypoestes forskaolii* (s2) 0.5%, *Melhania virescens* (s2) 0.5%, *Aizoon virgatum* (s2) 0.2%, *Lantana angolensis* (s2) 0.2%, *Mundulea sericea* (s2) 0.2%, *Seddera suffruticosa* (s2) 0.2%, *Boscia foetida* subsp. *foetida* (s2) 0.1%, *Chascanum pinnatifidum* (s2) 0.1%, *Commiphora pyracanthoides*

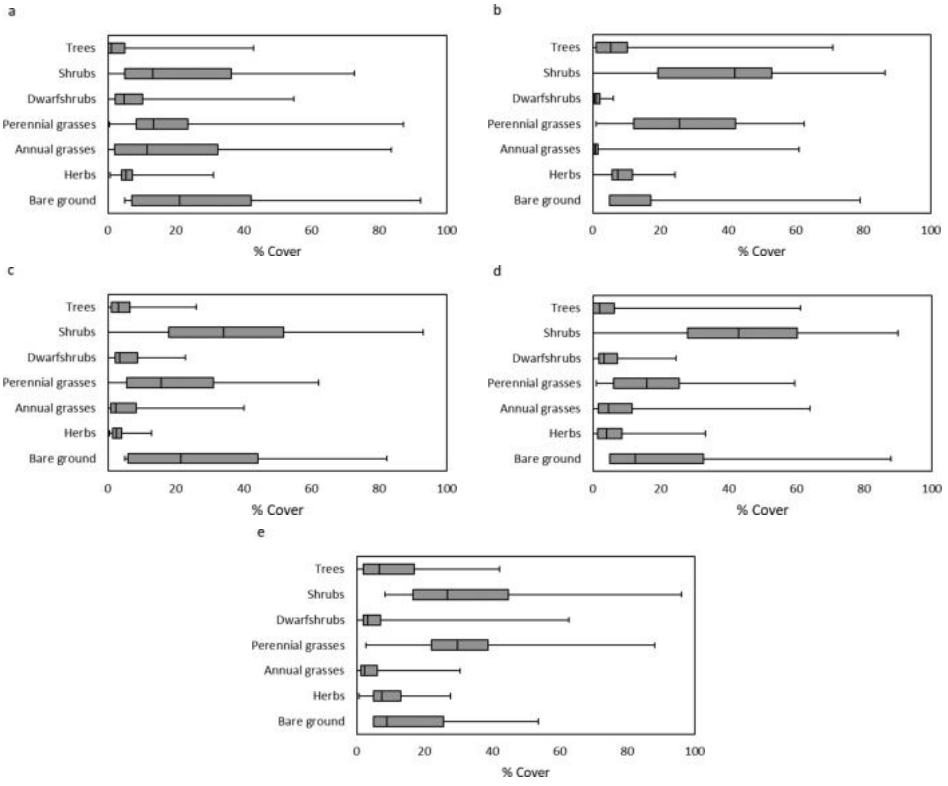

Figure 8. Typical structure of the associations of the Thornbush – Karstveld transition: (**a**) *Combreto hereroense-Tarchonanthoetum camphorati*; (**b**) *Aristido pilgeri-Vachellietum eriolobae*; (**c**) *Cenchro ciliaris-Senegalietum detinentis* typicum; (**d**) *Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae*; (**e**) *Eucleo undulatae-Oleetum africanae.*

(s2) 0.1%, *Helichrysum tomentosulum* (s2) 0.1%, *Hibiscus caesius* (s2) 0.1%, *Enneapogon scoparius* (gp) 5%, *Eragrostis echinochloidea* (gp) 5%, *Heteropogon contortus* (gp) 2%, *Cenchrus ciliaris* (gp) 0.5%, *Fingerhuthia africana* (gp) 0.5%, *Dichanthium annulatum* var. *papillosum* (gp) 0.2%, *Stipagrostis hirtigluma* (ga) 15%, *Indigofera charlieriana* (hl) 0.1%, *Ocimum americanum* var. *americanum* (hl) 0.1%, *Sericorema sericea* (hl) 0.1%

Constant species: *Senegalia mellifera* subsp. *detinens*, *Combretum hereroense*, *Grewia flava*, *Dichrostachys cinerea*, *Melhania virescens*, *Vachellia reficiens / luederitzii*, *Eragrostis echinochloidea*, *Tarchonanthus camphoratus*

Strohbach (2002) described this subassociation as her *Acacia mellifera - Stipagrostis hirtigluma* community. Typically, the *Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae* forms a closed tall shrubland, dominated by the phanerophytes *Senegalia mellifera* subsp. *detinens*, *Vachellia reficiens / luederitzii*, *Dichrostachys cinerea*, *Terminalia prunioides*, *Tarchonanthus camphoratus*, *Croton gratissimus*, *Combretum imberbe*, *Catophractes alexandri*, *Vachellia karroo* and *Combretum hereroense*. The grass sward is dominated by *Stipagrostis hirtigluma* subsp. *hirtigluma*, *Eragrostis trichophora*, *Eragrostis echinochloidea*, *Enneapogon scoparius*, *Enneapogon desvauxii*, *Cenchrus ciliaris*, *Urochloa brachyura*, *Stipagrostis uniplumis* var. *uniplumis*, *Sporobolus ioclados*, *Setaria pumila*, *Microchloa caffra*, *Melinis repens* subsp. *grandiflora*, *Heteropogon contortus*, *Eragrostis rigidior*, *Eragrostis porosa*, *Eragrostis nindensis*, *Eragrostis lehmanniana* and *Enneapogon cenchroides*. Conspicuous dwarfshrubs include *Petalidium englerianum*, *Monechma spartioides* and *Monechma genistifolium*. The vegetation is often densely encroached with a weak grass sward (Strohbach 2002) (Figures 8d, 9d).

The soils consist of sandy loam and sandy clay loam, often mollic Leptosols or petric Calcisols (Strohbach 2002). Stone cover is more prominent, reaching up to 5% medium-sized stones. The topography is gently undulating, but some relevés have been sampled in rolling landscapes. The altitude ranges between 1160 and 1850 m a.s.l.

Figure 9. Typical views of the associations of the Thornbush – Karstveld transition: (**a**) *Combreto hereroense-Tarchonanthoetum camphorati*, relevé 7987; (**b**) *Aristido pilgeri-Vachellietum eriolobae*, relevé 7804; (**c**) *Cenchro ciliaris-Senegalietum detinentis* typicum, relevé 3534; (**d**) *Cenchro ciliaris-Senegalietum detinentis stipagrostietosum hirtiglumae*, relevé 3521; (**e**) The *Cenchro ciliaris-Senegalietum detinentis* can degrade to this badly encroached state, relevé 7823; (**f**) *Eucleo undulatae-Oleetum africanae*, relevé 8001.

3.1.1.4 Eucleo undulatae-Oleetum africanae ass. nov.

Number of relevés: 32
Number of species observed: 189
Estimated number of species: 318
Type relevé: 8097 (holotypus), sampled on 15 April 2008 at 19.44583°S, 17.95917°E (Toggenberg)
Spirostachys africana (t1) 10%, *Elaeodendron transvaalense* (t2) 1%, *Vachellia luederitzii* (t3) 5%, *Commiphora glandulosa* (t3) 1%, *Senegalia mellifera* subsp. *detinens* (s1) 20%, *Croton gratissimus* var. *subgratissimus* (s1) 10%, *Olea europaea* subsp. *africana* (s1) 10%, *Euclea undulata* (s1) 5%, *Searsia marlothii* (s1) 2%, *Terminalia prunioides* (s1) 2%, *Commiphora africana* (s1) 1%, *Commiphora glandulosa* (s1) 1%, *Dombeya rotundifolia* (s1) 1%, *Flueggea virosa* (s1) 1%, *Mundulea sericea* (s1) 1%, *Vachellia nilotica* (s1) 1%, *Lantana angolensis* (s2) 1%, *Aerva leucura* (s2) 0.5%, *Fingerhuthia africana* (gp) 5%, *Enneapogon scoparius* (gp) 2%, *Eragrostis echinochloidea* (gp) 2%, *Eragrostis rigidior* (gp) 2%, *Heteropogon contortus* (gp) 2%, *Andropogon chinensis* (gp) 1%, *Anthephora pubescens* (gp) 1%, *Cenchrus ciliaris* (gp) 1%, *Eragrostis nindensis* (gp) 1%, *Oropetium capense* (gp) 1%, *Urochloa oligotricha* (gp) 1%, *Cymbopogon pospischilii* (gp) 0.5%, *Digitaria eriantha* (gp) 0.5%, *Eustachys paspaloides* (gp) 0.5%, *Enneapogon cenchroides* (ga) 10%, *Eragrostis porosa* (ga) 10%, *Aristida effusa* (ga) 5%, *Aristida rhiniochloa* (ga) 2%, *Enneapogon desvauxii* (ga) 2%, *Melinis repens* subsp. *grandiflora* (ga) 2%, *Brachiaria malacodes* (ga) 1%, *Tragus racemosus* (ga) 0.5%, *Cyperus amabilis* (hl) 2%, *Blepharis obmitrata* (hl) 1%, *Buchnera hispida* (hl) 1%, *Calostephane divaricata* (hl) 1%, *Achyranthes aspera* var. *sicula* (hl) 0.5%, *Aptosimum lineare* (hl) 0.5%, *Commelina benghalensis* (hl) 0.5%, *Geigeria ornativa* (hl) 0.5%, *Heliotropium ovalifolium* (hl) 0.5%, *Hibiscus calyphyllus* (hl) 0.5%, *Indigofera charlieriana* (hl) 0.5%, *Kohautia aspera* (hl) 0.5%, *Melhania virescens* (hl) 0.5%, *Monechma spartioides* (hl) 0.5%, *Pavonia burchellii* (hl) 0.5%, *Pentarrhinum insipidum* (hl) 0.5%, *Pupalia lappacea* (hl) 0.5%, *Sericorema sericea* (hl) 0.5%, *Tagetes minuta* (hl) 0.5%, *Tephrosia dregeana* var. *dregeana* (hl) 0.5%

Diagnostic species: *Olea europaea* subsp. *africana,* *Fingerhuthia africana*, *Digitaria eriantha*, *Euclea undulata*, *Croton gratissimus*, *Kohautia aspera*

Constant species: *Senegalia mellifera* subsp. *detinens, Heteropogon contortus, Vachellia reficiens / luederitzii, Melhania virescens, Searsia marlothii, Combretum hereroense,* *Eragrostis echinochloidea*, *Ziziphus mucronata*, *Enneapogon scoparius*, *Lantana angolensis*, *Cenchrus ciliaris*, *Tarchonanthus camphoratus*, *Seddera suffruticosa*, *Hibiscus caesius*, *Grewia flava*, *Dichrostachys cinerea*, *Anthephora pubescens*

The *Eucleo undulatae-Oleetum africanae* forms a short, moderately closed thicket dominated by the phanerophytes *Senegalia mellifera* subsp. *detinens*, *Olea europaea* subsp. *africana*, *Vachellia reficiens / luederitzii*, *Dichrostachys cinerea*, *Combretum imberbe*, *Combretum hereroense*, *Euclea undulata* and *Catophractes alexandri*. The grass sward consists of predominantly *Enneapogon desvauxii*, *Heteropogon contortus*, *Urochloa oligotricha*, *Stipagrostis uniplumis* var. *uniplumis*, *Fingerhuthia africana*, *Enneapogon scoparius*, *Cenchrus ciliaris*, *Eragrostis trichophora* and *Eragrostis echinochloidea* (Figures 8e, 9f).

This association occurs on the southern footslopes and pedeplains of the Otavi mountain range. It is especially widespread around Otavi but is found also elsewhere along the mountain range as far east as Gaikos mountain. The soils are described as medium-textured, dark Leptosols on calcretes (Coetzee et al. 1998). Stone cover consists of a mixture of gravel, small, medium and large stones (calcretes) up to 30% cover. The slopes are gently undulating to undulating, at an altitudinal range of between 1300 and 1540 m a.s.l.

4. Kalahari

Pockets of Kalahari sand deposits are found within the Otavi Mountain range, supporting vegetation typical for the Woodland savanna of the northern Kalahari *sensu* Giess (1998). Within the present study area, the Kalahari vegetation is dominated by the families *Poaceae* (57 species) and *Fabaceae* (54 species). All other families are represented by 15 or less species. An abbreviated synoptic table is presented in Table 4, whilst the full synoptic table is available in Suppl. material 3.

Overview of the Kalahari associations:
4.1 Undefined upper hierarchy
4.1.1.1 *Terminalio sericeae-Schinziophyetum rautanenii*
4.1.1.2 *Combreto collini-Terminalietum sericeae*
4.1.1.3 *Senegalio cinereae-Peltophoretum africanae*
4.1.1.4 *Terminalietum sericeo-prunioidis*

4.1.1.1 Terminalio sericeae-Schinziophyetum rautanenii B. Strohbach 2014

Number of relevés: 11
Number of species observed: 72
Estimated number of species: 106
Average species density in 1000 m^2: 30
Type relevé: 4013 (holotypus), designated by Strohbach (2014). Sampled on 26 March 1992 at 19.42139°S, 18.38889°E (Gaikos).
Schinziophyton rautanenii (t1) 2a, *Pterocarpus angolensis* (t1) +, *Burkea africana* (t2) 1, *Combretum collinum* (t2) +, *Lannea discolor* (t2) r, *Peltophorum africanum* (t3) +, *Croton gratissimus* var. *gratissimus* (s1) 2b, *Terminalia sericea* (s1) 2b, *Bauhinia petersiana* subsp. *macrantha* (s1) +, *Grewia olukondae* (s1) +, *Ochna pulchra* (s2) +, *Strychnos pungens* (s2) r, *Eragrostis trichophora* (gp) 1, *Melinis repens* subsp. *repens* (gp) +, *Panicum maximum* (gp) +, *Stipagrostis uniplumis* var. *uniplumis* (gp) +, *Aristida stipitata* subsp. *stipitata* (ga) 3, *Melinis repens* subsp. *grandiflora* (ga) +, *Tricholaena monachne* (ga) +, *Erlangea misera* (hl) 1, *Bidens biternata* (hl) +, *Blepharis obmitrata* (hl) +, *Cyperus margaritaceus* (hl) +, *Hibiscus vitifolius* (hl) +, *Hypoestes forskaolii* (hl) +, *Indigofera daleoides* (hl) +, *Indigofera flavicans* (hl) +, *Monechma debile* (hl) +, *Phyllanthus maderaspatensis* (hl) +, *Rhynchosia sublobata* (hl) +, *Sida ovata* (hl) +, *Tephrosia dregeana* var. *dregeana* (hl) +, *Thunbergia aurea* (hl) +

Diagnostic species: *Grewia olukondae, Tricholaena monachne, Monechma debile,* *Schinziophyton rautanenii*, *Pterocarpus angolensis*, *Indigofera daleoides*, *Phyllanthus maderaspatensis*, *Aristida stipitata*, *Strychnos pungens*, *Hibiscus vitifolius*, *Combretum collinum*, *Chamaecrista biensis*, *Burkea africana*, *Ochna pulchra*

Table 4. Abbreviated synoptic table for the Kalahari vegetation, showing all species occurring in more than 10% of relevés of this group, with fidelity (phi coefficient × 100) and frequency of occurrence (%).

Association	**4.1.1.1**		**4.1.1.2**		**4.1.1.3**		**4.1.1.4**	
No of relevés	**11**		**25**		**15**		**21**	
Species	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**
Grewia olukondae	69	100	---	28	---	0	---	38
Tricholaena monachne	65	55	---	4	---	0	---	0
Monechma debile	62	45	---	0	---	0	---	0
Schinziophyton rautanenii	56	45	---	0	---	7	---	0
Pterocarpus angolensis	55	36	---	0	---	0	---	0
Indigofera daleoides	51	64	---	12	---	20	---	5
Phyllanthus maderaspatensis	51	64	---	24	---	0	---	14
Aristida stipitata	48	91	---	52	---	20	---	33
Hibiscus vitifolius	47	27	---	0	---	0	---	0
Strychnos pungens	47	27	---	0	---	0	---	0
Chamaecrista biensis	42	36	---	8	---	0	---	5
Burkea africana	42	45	---	12	---	13	---	0
Ochna pulchra	41	64	---	32	---	27	---	0
Jacquemontia tamnifolia	---	9	76	80	---	7	---	0
Calostephane divaricata	---	0	61	44	---	0	---	0
Ozoroa schinzii	---	9	59	52	---	0	---	0
Combretum engleri	---	9	56	48	---	0	---	0
Phyllanthus omahakensis	---	0	55	36	---	0	---	0
Acanthosicyos naudinianus	---	0	54	56	---	7	---	14
Schmidtia kalahariensis	---	0	48	28	---	0	---	0
Megaloprotachne albescens	---	0	44	24	---	0	---	0
Polydora steetziana	---	0	42	44	---	0	---	24
Bauhinia petersiana subsp. *macrantha*	---	64	40	84	---	40	---	10
Grewia flavescens	---	0	---	56	62	100	---	29
Pavonia burchellii	---	0	---	4	59	47	---	0
Limeum sulcatum	---	0	---	0	56	53	---	14
Senegalia ataxacantha	---	36	---	60	53	93	---	0
Commelina benghalensis	---	0	---	4	51	47	---	10
Ziziphus mucronata	---	0	---	4	50	53	---	19
Ipomoea welwitschii	---	0	---	0	47	33	---	5
Chamaecrista absus	---	0	25	52	43	67	---	10
Tarchonanthus camphoratus	---	0	---	0	40	27	---	5
Terminalia prunioides	---	0	---	32	---	13	65	86
Combretum hereroense	---	0	---	0	---	7	53	43
Seddera suffruticosa	---	0	---	0	---	0	48	29
Senegalia mellifera subsp. *detinens*	---	18	---	16	---	67	45	86
Aristida rhiniochloa	---	0	---	12	---	7	44	43
Hyphaene petersiana	---	9	---	0	---	0	43	33
Boscia albitrunca	---	0	---	4	---	7	41	33
Combretum collinum	45	82	57	92	---	0	---	0
Terminalia sericea	---	91	---	96	---	93	---	67
Dichrostachys cinerea	---	55	---	80	---	87	29	100
Urochloa brachyura	---	55	---	84	---	87	---	95
Stipagrostis uniplumis var. *uniplumis*	---	82	---	80	---	60	---	86
Croton gratissimus	38	100	27	92	---	47	---	43
Combretum apiculatum	---	45	---	60	---	60	32	90
Senegalia cinerea	---	45	---	68	---	87	---	62
Melinis repens subsp. *grandiflora*	---	64	30	88	---	47	---	52
Grewia bicolor	---	27	---	64	---	60	27	81
Pogonarthria fleckii	---	18	37	84	---	27	33	81
Commiphora glandulosa	---	36	---	64	---	53	---	67
Peltophorum africanum	---	36	---	16	32	80	28	76
Eragrostis dinteri	---	55	33	68	---	0	---	38
Commiphora angolensis	---	9	40	64	---	40	---	14
Vachellia erioloba	---	18	25	52	---	20	---	38
Oxygonum alatum	---	18	26	52	---	27	---	29
Melhania acuminata	---	18	---	20	32	60	---	38
Grewia flava	---	0	---	40	---	33	---	33
Limeum fenestratum	---	45	---	40	---	7	---	24
Schmidtia pappophoroides	---	18	---	28	---	20	---	43
Tephrosia dregeana var. *dregeana*	---	18	---	28	---	47	---	24
Clerodendrum ternatum	---	18	---	24	---	47	---	24
Philenoptera nelsii	---	0	---	40	---	33	---	24
Eragrostis rigidior	---	0	---	12	---	40	35	52
Aristida adscensionis	---	36	31	48	---	0	---	14
Bidens biternata	---	36	---	20	30	53	---	10

Association	4.1.1.1		4.1.1.2		4.1.1.3		4.1.1.4	
No of relevés	11		25		15		21	
Species	phi	%	phi	%	phi	%	phi	%
Combretum psidioides	33	55	---	32	---	13	---	14
Evolvulus alsinoides	---	9	---	28	---	13	27	43
Digitaria seriata	---	18	---	36	---	13	---	29
Ximenia americana	35	55	---	20	---	7	---	29
Rhynchosia venulosa	40	64	---	8	---	40	---	14
Syncolostemon bracteosus	---	9	29	44	---	33	---	5
Vachellia reficiens / luederitzii	---	0	---	24	---	13	37	48
Sida ovata	---	27	---	32	---	13	---	19
Eragrostis trichophora	---	36	---	16	---	7	---	33
Searsia tenuinervis	---	36	---	20	---	13	---	24
Waltheria indica	---	9	---	12	---	33	---	33
Asparagus nelsii	---	0	---	32	---	27	---	19
Mundulea sericea	---	27	---	24	---	20	---	14
Bulbostylis hispidula	---	0	29	36	---	13	---	19
Xenostegia tridentata subsp. *angustifolia*	---	0	37	40	---	7	---	19
Tragus berteronianus	---	9	---	28	---	7	---	24
Cyperus margaritaceus	---	27	---	8	24	40	---	14
Enneapogon cenchroides	---	0	34	36	---	0	---	24
Lantana angolensis	---	0	---	16	---	27	---	29
Panicum maximum	---	36	---	28	---	7	---	5
Commelina africana	---	36	---	12	---	27	---	10
Albizia anthelmintica	---	0	---	24	---	20	---	19
Commiphora africana	---	0	29	32	---	7	---	19
Tephrosia purpurea	---	0	30	32	---	0	---	24
Eragrostis lehmanniana	---	0	---	28	35	40	---	0
Dicoma tomentosa	---	0	---	8	---	20	34	38
Kyphocarpa angustifolia	---	9	---	20	---	7	---	24
Melinis repens subsp. *repens*	---	27	---	0	---	33	---	19
Triraphis schinzii	---	18	---	4	---	20	---	29
Aristida congesta subsp. *congesta*	---	9	---	12	---	0	38	38
Phyllanthus pentandrus	---	0	---	8	36	40	---	19
Cyperus amabilis	---	0	---	28	---	13	---	14
Cleome rubella	---	0	---	12	---	33	---	19
Heteropogon melanocarpus	---	0	34	32	---	13	---	5
Acrotome angustifolia	---	0	37	32	---	0	---	14
Gisekia africana	---	0	---	12	---	27	---	19
Rhynchosia totta	---	0	---	24	---	7	---	19
Sporobolus panicoides	---	0	---	12	---	20	---	24
Vachellia nilotica	---	0	---	12	---	13	---	29
Zornia milneana	---	0	---	12	30	33	---	14
Aristida pilgeri	---	0	---	0	---	20	39	38
Blepharis obmitrata	---	27	---	12	---	0	---	19
Thunbergia aurea	---	27	---	8	25	33	---	0
Blepharis maderaspatensis	---	27	---	4	---	27	---	10
Tephrosia lupinifolia	---	9	36	32	---	7	---	0
Spermacoce senensis	---	0	---	16	33	33	---	5
Dicoma schinzii	---	9	---	20	---	7	---	10
Sesamum triphyllum	---	9	24	24	---	7	---	5
Ximenia caffra	---	9	---	12	33	33	---	0
Setaria pumila	---	9	---	0	32	33	---	14
Spirostachys africana	---	0	---	8	---	13	---	24
Monechma spartioides	---	0	---	4	---	20	---	24
Combretum imberbe	---	0	---	0	---	20	29	29
Erlangea misera	40	36	---	16	---	0	---	0
Indigofera flavicans	38	36	---	12	---	7	---	0
Asparagus exuvialis	---	0	---	16	---	0	---	19
Gymnosporia senegalensis	---	0	---	0	---	13	34	29

Constant species: *Croton gratissimus, Terminalia sericea, Stipagrostis uniplumis* var. *uniplumis,* *Rhynchosia venulosa*, *Melinis repens* subsp. *grandiflora*, *Bauhinia petersiana* subsp. *macrantha*

The *Terminalio sericeae-Schinziophyetum rautanenii* forms a tall, moderately closed woodland dominated by *Terminalia sericea*, *Combretum apiculatum*, *Senegalia cinerea*, *Pterocarpus angolensis*, *Croton gratissimus*, *Combretum collinum* and *Schinziophyton rautanenii.* The grass sward is not well developed, featuring *Aristida stipitata*, *Stipagrostis uniplumis* var. *uniplumis* and *Melinis repens* subsp. *grandiflora*. Other than the conspicuous presence of the tall tree species *Pterocarpus angolensis* and *Schinziophyton rautanenii*, the composition resembles that of the *Combreto collini-Terminalietum sericeae* (Figure 10a).

The *Terminalio sericeae-Schinziophyetum rautanenii* has especially been found on east-facing sand ramps of aeolian origin (Lancaster and Tchakerian 1996; Rowell et al. 2017) in the Gaikos and Kokasib mountains north-east of Grootfontein. The topography is gently undulating with no stone cover, at an altitudinal range of between 1190 and 1350 m a.s.l.

4.1.1.2 Combreto collini-Terminalietum sericeae B. Strohbach 2014

Number of relevés: 25
Number of species observed: 127
Estimated number of species: 213
Average species density in 1000 m²: 41
Diagnostic species: ***Jacquemontia tamnifolia, Calostephane divaricata,*** *Ozoroa schinzii*, *Combretum collinum*, *Combretum engleri*, *Phyllanthus omahakensis*, *Acanthosicyos naudinianus*, *Schmidtia kalahariensis*, *Megaloprotachne albescens*, *Polydora steetziana*, *Bauhinia petersiana* subsp. *macrantha*
Constant species: ***Terminalia sericea, Croton gratissimus, Melinis repens*** **subsp.** ***grandiflora, Urochloa brachyura, Pogonarthria fleckii,*** *Stipagrostis uniplumis* var. *uniplumis*, *Dichrostachys cinerea*, *Senegalia cinerea*, *Eragrostis dinteri*, *Grewia bicolor*, *Commiphora glandulosa*, *Commiphora angolensis*

The *Combreto collini-Terminalietum sericeae* forms a short, moderately closed bushland dominated by the phanerophytes *Terminalia sericea*, *Croton gratissimus*, *Bauhinia petersiana* subsp. *macrantha*, *Combretum psidioides*, *Combretum collinum* and *Grewia olukondae*. The grass sward is dominated by *Aristida stipitata*, *Schmidtia kalahariensis*, *Megaloprotachne albescens*, *Eragrostis trichophora*, *Pogonarthria fleckii*, *Melinis repens* subsp. *grandiflora*, *Eragrostis rigidior* and *Eragrostis dinteri*, with *Polydora steetziana* a conspicuous annual herb in the matrix (Figures 10b, 11a).

The *Combreto collini-Terminalietum sericeae* occurs on the Kalahari dune belt east and north of the Omuramba Ovambo. The presence of *Combretum apiculatum*, *Vachellia tortilis* subsp. *heteracantha* and *Terminalia prunioides* indicates the proximity to true Karstveld vegetation. This could possibly result in the recognition of a further subassociation of this very wide-spread association (cf. Strohbach 2014a) during a future review of the Kalahari types. The topography is gently undulating dune field with no stone cover, with an altitudinal range of between 1100 and 1300 m a.s.l.

4.1.1.3 *Senegalio cinereae-Peltophoretum africanae* ass. nov.

Number of relevés: 15
Number of species observed: 141
Estimated number of species: 244
Average species density in 1000 m²: 40
Type relevé: 8000 (holotypus), sampled on 12 March 2008 at 19.55588°S, 17.14389°E (Gobas Pforte)
Combretum imberbe (t3) 5%, *Commiphora tenuipetiolata* (t3) 1%, *Terminalia sericea* (t2) 20%, *Combretum apiculatum* subsp. *apiculatum* (t2) 5%, *Spirostachys africana* (t2) 2%, *Pavetta zeyheri* (s2) 0.5%, *Dichrostachys cinerea* (s1) 10%, *Grewia flavescens* (s1) 10%, *Senegalia ataxacantha* (s1) 10%, *Senegalia cinerea* (s1) 10%, *Grewia bicolor* (s1) 5%, *Peltophorum africanum* (s1) 5%, *Rhigozum brevispinosum* (s1) 2%, *Ziziphus mucronata* (s1) 2%, *Senegalia mellifera* subsp. *detinens* (s1) 1%, *Commiphora angolensis* (s1) 0.5%, *Croton gratissimus* var. *subgratissimus* (s1) 0.5%, *Eragrostis lehmanniana* var. *lehmanniana* (gp) 1%, *Eragrostis porosa* (ga) 10%, *Setaria pumila* (ga) 10%, *Urochloa brachyura* (ga) 10%, *Tragus racemosus* (ga) 2%, *Brachiaria deflexa* (ga) 1%, *Aristida stipoides* (ga) 0.5%, *Melinis repens* subsp. *grandiflora* (ga) 0.5%, *Spermacoce senensis* (hl) 5%, *Achyranthes aspera* var. *sicula* (hl) 2%, *Bidens biternata* (hl) 2%, *Chamaecrista absus* (hl) 1%, *Ipomoea sinensis* (hl) 1%, *Cleome rubella* (hl) 0.5%, *Crassocephalum coeruleum* (hl) 0.5%, *Cyperus amabilis* (hl) 0.5%, *Erucastrum arabicum* (hl) 0.5%, *Euphorbia inaequilatera* (hl) 0.5%, *Gisekia africana* (hl) 0.5%, *Limeum sulcatum* (hl) 0.5%, *Melhania acuminata* (hl) 0.5%, *Pavonia burchellii* (hl) 0.5%, *Phyllanthus pentandrus* (hl) 0.5%, *Sesamum triphyllum* (hl) 0.5%, *Solanum lichtensteinii* (hl) 0.5%, *Zornia milneana* (hl) 0.5%

Diagnostic species: ***Grewia flavescens,*** *Pavonia burchellii*, *Limeum sulcatum*, *Senegalia ataxacantha*, *Commelina benghalensis*, *Ziziphus mucronata*, *Ipomoea welwitschii*, *Chamaecrista absus*, *Tarchonanthus camphoratus*

Constant species: ***Terminalia sericea, Urochloa brachyura, Senegalia cinerea, Dichrostachys cinerea,*** *Peltophorum africanum*, *Senegalia mellifera* subsp. *detinens*

The *Senegalio cinereae-Peltophoretum africanae* forms a tall, moderately closed to closed thicket, dominated by the phanerophytes *Terminalia sericea*, *Senegalia cinerea*, *Senegalia ataxacantha*, *Peltophorum africanum*, *Dichrostachys cinerea*, *Croton gratissimus* and *Combretum apiculatum*. These are accompanied by the grasses *Urochloa brachyura*, *Setaria pumila* and *Eragrostis rigidior* (Figures 10c, 11b). Conspicuous is the mix of psammophilous species (*Terminalia sericea*, *Senegalia ataxacantha*), species preferring a loamier habitat (*Senegalia cinerea*, *Peltophorum africanum*) and species known for their preference of stony or rocky habitats (*Combretum apiculatum*). This is indicative of the habitat of the *Senegalio cinereae-Peltophoretum africanae*, being sand deposits within the Otavi mountain range. The soils consist of loose aeolian sand, are variably deep, over a rocky substrate of limestone or dolomite of the Otavi Group. Stone cover is low, with no gravel, up to 2% small, medium and large stones, but up to 40% rocks (see Figure 11c). As with most Kalahari deposits, the slopes are gently undulating, seldom rolling. The association occurs at an altitudinal range of between 1200 and 1500 m a.s.l.

4.1.1.4 Terminalietum sericeo-prunioidis ass. nov.

Number of relevés: 21
Number of species observed: 157
Estimated number of species: 273
Average species density in 1000 m²: 38
Type relevé: 8131 (holotypus), sampled on 18 April 2008 at 18.80028°S, 17.88139°E (Rushof)
Terminalia prunioides (t2) 10%, *Hyphaene petersiana* (t2) 5%, *Vachellia erioloba* (t2) 2%, *Spirostachys africana* (t2) 1%, *Combretum apiculatum* subsp. *apiculatum* (t3) 10%, *Combretum imberbe* (t3) 2%, *Commiphora glandulosa* (t3) 2%, *Terminalia sericea* (t3) 1%, *Vachellia luederitzii* (t3) 1%, *Senegalia mellifera* subsp. *detinens* (s2) 1%, *Grewia bicolor* (s1) 10%, *Combretum hereroense* (s1) 5%, *Grewia flavescens* (s1) 5%, *Ximenia americana* (s1) 2%, *Croton gratissimus* var. *subgratissimus* (s1) 1%, *Dichrostachys cinerea* (s1) 1%, *Elaeodendron transvaalense* (s1) 1%, *Hyphaene petersiana* (s1) 1%, *Peltophorum africanum* (s1) 1%, *Ziziphus mucronata* (s2) 0.5%, *Eragrostis rigidior* (gp) 2%,

Stipagrostis uniplumis var. *uniplumis* (gp) 2%, *Triraphis schinzii* (gp) 1%, *Brachiaria nigropedata* (gp) 0.5%, *Fingerhuthia africana* (gp) 0.5%, *Heteropogon contortus* (gp) 0.5%, *Schizachyrium sanguineum* (gp) 0.5%, *Schmidtia pappophoroides* (gp) 0.5%, *Pogonarthria fleckii* (ga) 10%, *Aristida rhiniochloa* (ga) 2%, *Eragrostis dinteri* (ga) 2%, *Aristida effusa* (ga) 0.5%, *Enneapogon cenchroides* (ga) 0.5%, *Melinis repens* subsp. *grandiflora* (ga) 0.5%, *Urochloa brachyura* (ga) 0.5%, *Polydora steetziana* (hl) 10%, *Monechma spartioides* (hl) 5%, *Ocimum americanum* var. *americanum* (hl) 5%, *Cyperus amabilis* (hl) 1%, *Waltheria indica* (hl) 1%, *Acrotome angustifolia* (hl) 0.5%, *Aptosimum decumbens* (hl) 0.5%, *Blepharis obmitrata* (hl) 0.5%, *Dicoma tomentosa* (hl) 0.5%, *Evolvulus alsinoides* (hl) 0.5%, *Geigeria ornativa* (hl) 0.5%, *Gymnema sylvestre* (hl) 0.5%, *Heliotropium nelsonii* (hl) 0.5%, *Hermannia eenii* (hl) 0.5%, *Hibiscus caesius* (hl) 0.5%, *Kyllinga alata* (hl) 0.5%, *Kyphocarpa angustifolia* (hl) 0.5%, *Melhania acuminata* (hl) 0.5%, *Ocimum filamentosum* (hl) 0.5%, *Seddera suffruticosa* (hl) 0.5%, *Sida ovata* (hl) 0.5%, *Tephrosia purpurea* (hl) 0.5%, *Zornia milneana* (hl) 0.5%.

Diagnostic species: ***Terminalia prunioides,*** *Combretum hereroense*, *Seddera suffruticosa*, *Senegalia mellifera* subsp. *detinens*, *Aristida rhiniochloa*, *Hyphaene petersiana*, *Boscia albitrunca*

Constant species: ***Dichrostachys cinerea, Urochloa brachyura, Combretum apiculatum, Stipagrostis uniplumis*** **var.** ***uniplumis, Pogonarthria fleckii, Grewia bicolor,*** *Peltophorum africanum*, *Terminalia sericea*, *Commiphora glandulosa*, *Senegalia cinerea*

The *Terminalietum sericeo-prunioidis* forms a short, moderately closed bushland. It is dominated by the phanerophytes *Combretum apiculatum*, *Dichrostachys cinerea* and *Terminalia prunioides*, with *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis rigidior* and *Aristida pilgeri* forming the grass sward (Figures 10d, 11c). The unique combination of *Terminalia sericea* and *Terminalia prunioides* occurring together in the same stand is indicative of the habitat: the *Terminalietum sericeo-prunioidis* occurs on sandy flood plains adjacent to the Omuramba Ovambo, mostly on the western and southern sides of the Omuramba. The topography is flat and the altitude ranges from 1160 to 1500 m a.s.l.

5. The Karstveld proper: *Terminalietea prunioidis* cl. nov.

Synopsis:
Number of relevés: 330
Holotypus: *Terminalietalia prunioidis* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 640
Diagnostic species: *Terminalia prunioides*, *Spirostachys africana*, *Combretum apiculatum*, *Vachellia nilotica*, *Grewia villosa*, *Grewia bicolor*
Constant species: ***Dichrostachys cinerea,*** *Senegalia mellifera* subsp. *detinens*, *Commiphora glandulosa*, *Melinis repens* subsp. *grandiflora*, *Urochloa brachyura*, *Croton gratissimus*, *Grewia flavescens*, *Combretum imberbe*

The Karstveld *sensu* Giess (1998) is recognised as a vegetation class, dominated by trees and tall shrubs of *Terminalia prunioides*. The designated type for this class are the *Terminalietalia prunioidis*, representing the Karstveld plains to the north and west of the Otavi mountain range. A second order, the *Commiphoro glaucescentis-Kirkietalia acuminatae* (see below), is also recognised within this class. The vegetation is dominated by the plant families *Poaceae* (102 species), *Fabaceae* (76 species) and *Asteraceae* (36 species). An abbreviated synoptic table is presented in Table 5, whilst the full synoptic table is available in Suppl. material 3.

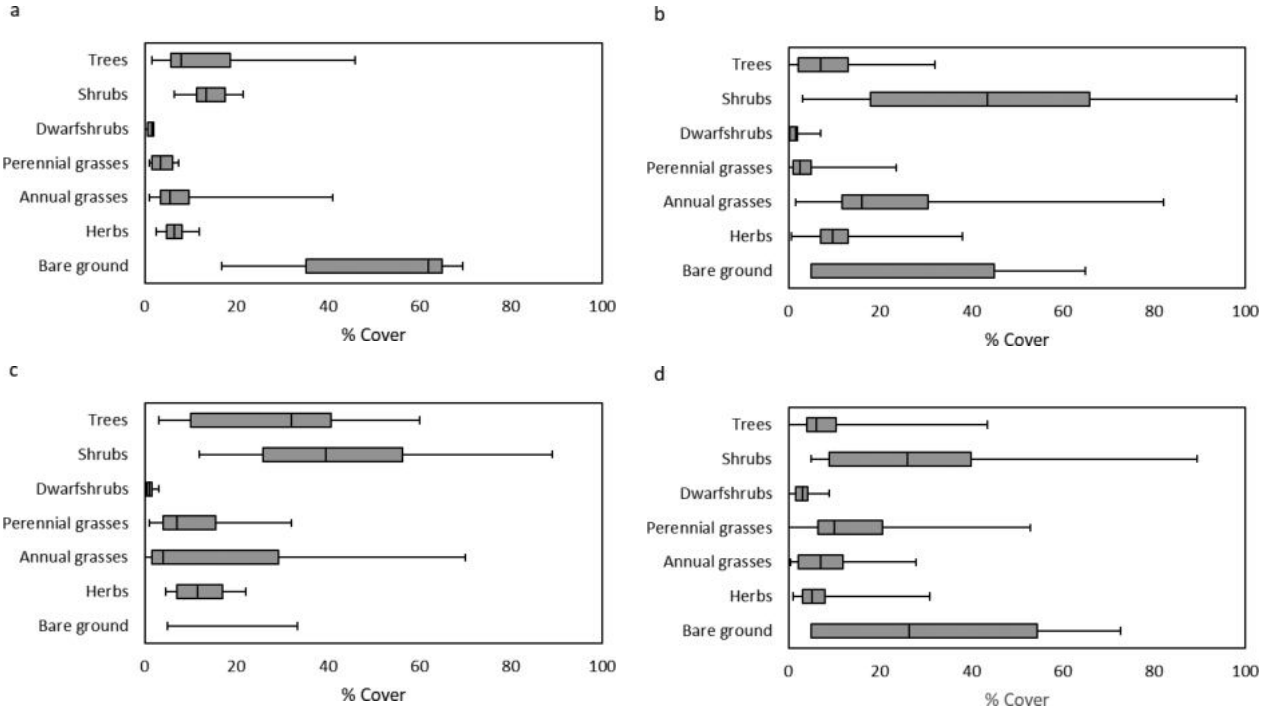

Figure 10. Typical structure of the associations of the Kalahari habitats included in the Karstveld: (**a**) *Terminalio sericeae-Schinziophyetum rautanenii*; (**b**) *Combreto collini-Terminalietum sericeae*; (**c**) *Senegalio cinereae-Peltophoretum africanae*; (**d**) *Terminalietum sericeo-prunioidis*.

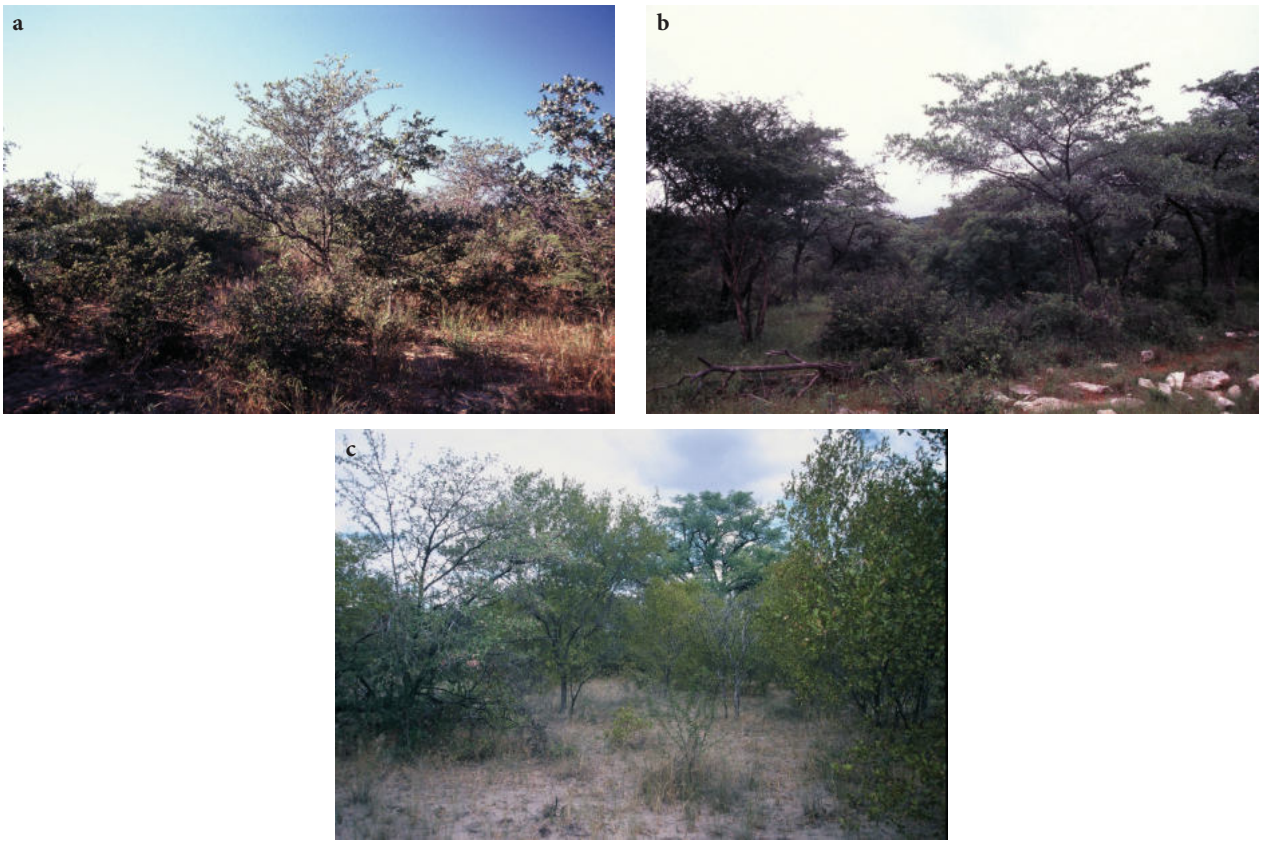

Figure 11. Typical views of the associations of the Kalahari habitats included in the Karstveld: (**a**) *Combreto collini-Terminalietum sericeae*, relevé 8120; (**b**) *Senegalio cinereae-Peltophoretum africanae*, relevé 7999; (**c**) *Terminalietum sericeo-prunioidis*, relevé 2783.

Overview of the *Terminalietea prunioidis*:
5.1 *Commiphoro glaucescentis-Kirkietalia acuminatae*
5.1.1 *Commiphoro glaucescentis-Kirkion acuminatae*
5.1.1.1 *Lanneo discoloris-Kirkietum acuminatae*
5.1.1.2 *Commiphoro glaucescentis-Kirkietum acuminatae*
5.1.1.3 *Commiphoro glaucescentis-Combretetum apiculati*
5.2 *Terminalietalia prunioidis*
5.2.1 Unnamed group
5.2.1.1 *Trago pedunculati-Ipomoeetum adenioidis*
5.2.1.2 *Combreto apiculati-Colophospermetum mopane*
5.2.2 *Terminalio prunioidis-Hyphaenion petersianae*
5.2.2.1 *Terminalio prunioidis-Hyphaenetum petersianae*
5.2.3 *Dichrostachyo cinereae-Terminalion prunioidis*
5.2.3.1 *Terminalio prunioidis-Spirostachyetum africanae*
5.2.3.2 *Dichrostachyo cinereae-Terminalietum prunioidis*

***5.1 Commiphoro glaucescentis-Kirkietalia acuminatae* ord. nov.**

Number of relevés: 54
Holotypus: *Commiphoro glaucescentis-Kirkion acuminatae* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 228
Diagnostic species: *Commiphora glaucescens, Kirkia acuminata, Dombeya rotundifolia, Danthoniopsis dinteri*
Constant species: *Combretum apiculatum*

The *Commiphoro glaucescentis-Kirkietalia acuminatae* represent the mountain vegetation of the Karstveld. Various forms are known from as far afield as the Opuwo district in north-western Namibia (Viljoen 1980) as well as the Etosha National Park (Le Roux 1980), confirming that the Karstveld extends further west than covered in this paper. Within this study, three associations to *Commiphoro glaucescentis-Kirkion acuminatae* are described, with the *Commiphoro glaucescentis-Kirkietum acuminatae* designated as the type to the *Commiphoro glaucescentis-Kirkion acuminatae*, which in turn is the type to the order. There is no distinct altitudinal or aspect differentiation between these associations, rather the rock type, steepness and massiveness of the substrate seems to be deterministic.

***5.1.1 Commiphoro glaucescentis-Kirkion acuminatae* all. nov.**

Number of relevés: 54
Type: *Commiphoro glaucescentis-Kirkietum acuminatae* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 228
Diagnostic species: *Commiphora glaucescens, Kirkia acuminata, Dombeya rotundifolia, Danthoniopsis dinteri*
Constant species: *Combretum apiculatum*

Table 5. Abbreviated synoptic table for the *Terminalietea prunioidis*, showing all species occurring in more than 10% of relevés of the class, with fidelity (phi coefficient × 100) and frequency of occurrence (%).

Order	**5.1 *Commiphoro glaucescentis-Kirkietalia acuminatae***						**5.2 *Terminalietalia prunioidis***									
Alliance	**5.1.1 *Commiphoro glaucescentis-Kirkion acuminatae***						**5.2.1**				**5.2.2 *Terminalio prunioidis-Hyphaenion petersianae***		**5.2.3 *Dichrostachyo cinereae-Terminalion prunioidis***			
Association	**5.1.1.1**		**5.1.1.2**		**5.1.1.3**		**5.2.1.1**		**5.2.1.2**		**5.2.2.1**		**5.2.3.1**		**5.2.3.2**	
No of relevés	**18**		**15**		**21**		**34**		**49**		**78**		**71**		**98**	
Species	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**	**phi**	**%**
Vangueria infausta	75	61	---	0	---	0	---	0	---	2	---	0	---	0	---	0
Pellaea calomelanos	68	50	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Cheilanthes dinteri	65	61	---	7	---	10	---	0	---	2	---	0	---	0	---	0
Lannea discolor	59	78	9	27	15	33	---	0	---	2	---	1	---	0	---	1
Cleome monophylla	55	39	---	0	---	0	---	0	---	0	---	0	---	1	---	4
Macrotyloma axillare	51	33	---	0	---	0	---	0	---	0	---	0	---	3	---	2
Ozoroa insignis	48	72	---	7	---	29	---	9	7	29	---	6	---	10	---	7
Andropogon gayanus var. *polycladus*	46	28	---	0	---	0	---	0	---	0	---	1	---	3	---	0
Merremia pinnata	43	22	---	0	---	0	---	0	---	0	---	1	---	0	---	0
Ipomoea verbascoidea	43	39	---	13	---	5	---	0	---	0	---	0	---	0	---	8
Thunbergia aurea	41	39	16	20	---	0	---	0	---	0	---	1	---	6	---	2
Danthoniopsis dinteri	40	61	64	87	---	5	---	0	---	2	---	0	---	0	---	1
Cissus nymphaeifolia	17	33	58	73	8	24	---	0	---	0	---	0	---	0	---	0
Steganotaenia araliacea var. *araliacea*	20	28	58	60	---	0	---	0	---	0	---	1	---	0	---	1
Ficus cordata	---	0	49	27	---	0	---	0	---	0	---	0	---	0	---	0
Crassocephalum coeruleum	---	0	47	27	---	0	---	0	---	0	---	0	---	1	---	1
Actiniopteris radiata	8	17	45	47	11	19	---	0	---	0	---	0	---	0	---	0
Berchemia discolor	---	0	44	47	---	5	---	9	---	10	---	3	2	13	---	0
Triraphis ramosissima	---	0	42	27	---	0	---	0	---	6	---	0	---	0	---	1
Momordica humilis	---	0	41	20	---	0	---	0	---	0	---	1	---	0	---	0
Boscia albitrunca	---	11	40	47	---	0	---	0	---	4	---	6	---	13	---	15
Fingerhuthia africana	---	0	---	0	64	71	---	0	---	10	---	4	---	0	11	23
Searsia marlothii	---	11	16	47	53	90	---	12	---	0	---	19	---	13	2	31
Dombeya rotundifolia	35	72	13	47	50	90	---	0	---	8	---	3	---	0	---	22
Anthephora pubescens	---	22	---	20	49	71	---	9	---	12	---	12	---	4	---	9
Eragrostis nindensis	---	44	---	33	45	100	4	47	12	57	---	15	---	3	---	34
Heteropogon contortus	14	56	---	20	45	95	---	12	---	39	---	40	---	13	---	31
Ophioglossum polyphyllum	---	0	---	0	43	29	---	0	---	2	---	1	---	0	---	5
Anthephora schinzii	---	0	---	0	---	0	66	76	19	33	---	0	---	6	---	2
Ipomoea adenioides	---	0	---	0	---	0	64	47	---	0	---	3	---	0	---	0
Tragus pedunculatus	---	0	---	0	---	0	59	38	---	0	---	0	---	0	---	0
Vahlia capensis	---	0	---	0	---	0	46	26	---	0	---	3	---	0	---	0
Pavetta zeyheri	---	6	---	0	---	24	44	62	---	4	---	18	---	13	---	14
Combretum hereroense	---	0	---	0	---	0	40	65	---	16	17	40	---	34	---	15
Colophospermum mopane	---	0	---	0	---	0	---	0	63	55	---	1	---	1	---	11
Setaria pumila	---	33	---	20	---	14	---	0	44	78	---	9	---	14	13	42
Aristida congesta subsp. *congesta*	---	0	---	0	---	0	---	0	---	0	58	40	---	1	---	1
Waltheria indica	---	6	---	0	---	0	---	0	---	0	50	42	---	7	---	5
Hyphaene petersiana	---	0	---	0	---	0	---	0	---	0	50	47	17	23	---	4
Stipagrostis uniplumis var. *uniplumis*	---	6	---	0	---	0	---	3	---	10	49	63	---	18	---	26
Schizachyrium exile	---	6	---	0	---	0	---	0	---	0	45	28	---	0	---	0
Kyphocarpa angustifolia	---	0	---	0	---	0	---	0	---	4	44	37	---	7	---	9
Schmidtia pappophoroides	---	6	---	0	---	5	---	0	---	2	43	36	---	3	---	4
Pogonarthria fleckii	---	11	---	0	---	0	---	6	23	43	43	63	---	11	---	16
Eragrostis rigidior	---	0	---	0	---	0	---	0	---	0	41	29	---	3	---	9
Spirostachys africana	---	11	---	20	---	14	---	3	---	43	26	67	43	89	---	30
Kirkia acuminata	50	94	54	100	4	38	---	0	---	12	---	1	---	10	---	7
Commiphora glaucescens	47	89	29	67	48	90	---	0	---	0	---	0	---	3	---	2
Terminalia prunioides	---	17	---	73	---	76	---	88	18	98	14	94	---	90	---	90
Dichrostachys cinerea	---	78	---	67	---	71	---	35	---	90	---	91	16	96	16	95
Combretum apiculatum	17	100	---	87	12	95	---	74	---	88	10	94	---	52	---	78
Grewia bicolor	---	44	---	67	---	48	---	62	---	69	13	83	18	90	---	78
Senegalia mellifera subsp. *detinens*	---	11	---	27	---	67	---	76	---	47	20	86	---	79	21	87
Commiphora glandulosa	---	28	---	67	---	62	13	79	18	86	---	72	---	45	---	59
Melinis repens subsp. *grandiflora*	14	83	---	73	---	52	13	82	13	82	---	60	---	41	---	53

Order	5.1 *Commiphoro glaucescentis-Kirkietalia acuminatae*						5.2 *Terminalietalia prunioidis*									
Alliance	5.1.1 *Commiphoro glaucescentis-Kirkion acuminatae*						5.2.1				5.2.2 *Terminalio prunioidis-Hyphaenion petersianae*		5.2.3 *Dichrostachyo cinereae-Terminalion prunioidis*			
Association	5.1.1.1		5.1.1.2		5.1.1.3		5.2.1.1		5.2.1.2		5.2.2.1		5.2.3.1		5.2.3.2	
No of relevés	18		15		21		34		49		78		71		98	
Species	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%
Croton gratissimus	26	100	15	87	26	100	6	76	---	39	---	32	---	52	---	63
Urochloa brachyura	---	28	---	20	---	10	---	21	20	71	28	82	23	75	---	53
Grewia flavescens	---	44	---	67	---	19	---	29	13	63	---	40	---	48	9	58
Vachellia nilotica	---	22	---	20	---	48	---	6	---	29	18	60	17	59	15	56
Combretum imberbe	---	6	---	40	---	52	15	62	---	45	10	55	---	45	---	36
Vachellia reficiens / luederitzii	---	0	---	0	---	48	---	21	---	16	---	38	21	56	27	63
Brachiaria deflexa	---	17	27	67	---	19	---	3	---	29	---	24	21	59	13	50
Aristida rhiniochloa	---	0	---	0	---	0	---	44	22	53	37	71	---	14	---	33
Tragus racemosus	---	0	---	13	---	24	---	44	15	47	---	32	---	32	---	36
Aristida adscensionis	---	33	---	13	---	5	23	59	12	45	12	45	---	24	---	21
Enneapogon cenchroides	---	6	---	27	---	10	---	44	---	31	---	21	16	46	---	38
Sporobolus panicoides	---	22	---	20	---	5	---	6	24	53	---	36	---	15	19	47
Bidens biternata	28	72	28	73	---	29	---	0	11	51	---	9	---	25	---	37
Grewia villosa	---	22	---	27	---	14	---	12	---	22	---	10	29	59	10	37
Mundulea sericea	13	56	---	27	25	71	38	88	---	18	---	21	---	14	---	18
Lantana angolensis	---	6	---	7	23	48	---	3	---	12	16	40	---	11	26	50
Enneapogon scoparius	---	11	---	33	26	57	---	12	---	24	---	15	---	18	15	45
Aristida effusa	---	6	---	33	---	14	---	18	---	29	---	29	---	17	10	34
Melhania acuminata	---	11	---	7	---	5	---	3	---	18	32	50	---	23	---	24
Seddera suffruticosa	---	0	---	7	---	19	---	6	---	22	18	36	---	13	21	39
Eragrostis porosa	---	6	---	40	---	5	20	47	21	49	---	4	---	21	---	27
Abutilon austro-africanum	---	17	---	7	---	14	---	3	---	20	---	8	32	52	11	31
Grewia flava	---	6	---	0	---	14	---	12	---	12	19	35	---	7	29	45
Commelina benghalensis	---	39	24	53	---	5	---	0	15	43	---	9	---	25	---	29
Euclea undulata	---	22	---	13	38	67	---	6	---	2	---	18	11	37	---	26
Tephrosia dregeana var. *dregeana*	---	11	---	33	---	19	---	32	---	27	---	24	---	24	---	17
Cenchrus ciliaris	---	22	---	20	---	38	---	0	---	27	---	4	---	17	21	44
Indigofera charlieriana	---	0	---	20	---	19	---	9	35	57	---	14	---	15	---	27
Melhania virescens	---	6	---	7	35	57	---	6	---	24	---	3	---	17	22	44
Pavonia burchellii	---	11	---	33	---	38	---	3	---	12	---	12	---	24	14	37
Achyranthes aspera var. *sicula*	21	50	29	60	---	10	---	3	---	20	---	6	10	38	---	20
Evolvulus alsinoides	---	6	---	7	---	0	---	3	---	20	35	49	---	17	---	20
Eragrostis trichophora	---	0	---	7	---	0	---	29	---	6	24	38	---	18	---	27
Gymnosporia senegalensis	---	6	---	20	---	38	---	26	---	8	---	22	9	31	---	18
Peltophorum africanum	28	50	---	20	---	10	---	3	---	4	19	41	---	17	---	20
Ocimum americanum var. *americanum*	---	0	---	0	---	5	28	44	---	8	28	44	---	15	---	15
Ziziphus mucronata	---	33	---	13	25	48	---	0	---	2	---	26	---	23	---	24
Otoptera burchellii	---	0	---	7	---	24	---	6	---	27	---	23	---	8	19	35
Phyllanthus pentandrus	15	44	28	60	---	33	---	15	---	20	---	3	---	17	---	24
Albizia anthelmintica	---	6	---	7	---	0	---	3	---	8	19	31	---	27	16	28
Ipomoea sinensis	---	0	---	7	---	5	---	0	38	51	---	12	---	20	13	28
Ocimum filamentosum	---	28	---	13	---	14	---	0	14	33	---	8	---	21	11	30
Acalypha segetalis	---	28	31	60	---	29	---	6	7	33	---	10	---	24	---	11
Kohautia aspera	---	0	---	7	---	5	---	12	36	49	---	9	---	11	15	30
Ximenia americana	36	61	---	7	---	29	---	9	---	4	---	18	10	32	---	13
Monechma spartioides	---	0	---	0	---	10	---	0	---	6	20	29	---	23	20	30
Enneapogon desvauxii	---	0	---	0	---	14	---	15	20	33	---	12	---	8	21	34
Sporobolus fimbriatus	---	11	---	7	---	10	---	0	---	6	39	50	---	23	---	7
Limeum sulcatum	---	6	---	27	---	0	---	12	15	31	---	15	---	18	---	18
Microchloa caffra	---	17	---	20	---	14	21	41	12	33	---	15	---	6	---	11
Flueggea virosa	---	11	29	53	15	38	---	9	---	24	---	4	---	17	---	18
Rhynchosia minima	---	22	---	20	16	33	---	0	---	12	---	6	---	18	10	28
Gisekia africana	---	11	---	7	---	0	23	38	---	24	---	10	---	24	---	11
Tragus berteronianus	---	0	---	13	---	0	---	3	16	27	---	17	---	17	13	23
Acrotome inflata	---	11	---	0	---	5	---	3	18	29	---	15	---	20	---	19
Pupalia lappacea	---	11	21	40	---	29	---	12	---	2	---	14	9	28	---	13
Helinus integrifolius	---	0	27	40	---	10	---	3	---	12	---	5	---	13	22	36

Order	5.1 *Commiphoro glaucescentis-Kirkietalia acuminatae*						5.2 *Terminalietalia prunioidis*									
Alliance	5.1.1 *Commiphoro glaucescentis-Kirkion acuminatae*						5.2.1				5.2.2 *Terminalio prunioidis-Hyphaenion petersianae*		5.2.3 *Dichrostachyo cinereae-Terminalion prunioidis*			
Association	5.1.1.1		5.1.1.2		5.1.1.3		5.2.1.1		5.2.1.2		5.2.2.1		5.2.3.1		5.2.3.2	
No of relevés	18		15		21		34		49		78		71		98	
Species	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%	phi	%
Eragrostis echinochloidea	---	0	---	0	---	29	38	53	---	10	---	9	---	8	---	21
Dicoma tomentosa	---	0	---	0	---	0	---	3	28	35	29	36	---	8	---	9
Rhynchosia totta	---	22	---	20	---	14	---	3	---	20	---	18	---	13	---	16
Commiphora tenuipetiolata	---	22	---	20	---	5	32	50	---	12	---	13	---	8	---	13
Setaria verticillata	---	0	---	27	---	0	---	0	---	0	---	14	27	35	---	20
Clerodendrum ternatum	---	0	---	13	---	14	---	3	---	14	12	23	---	8	13	23
Panicum maximum	29	44	---	20	---	5	---	3	---	0	---	17	15	31	---	11
Eragrostis lehmanniana	28	44	---	13	---	14	---	3	---	18	---	13	---	15	---	14
Sericorema sericea	---	0	---	0	---	5	18	29	27	37	---	8	---	10	---	16
Hibiscus caesius	---	0	---	13	---	29	---	0	---	4	---	9	---	15	19	29
Croton menyharthii	---	0	---	7	---	0	---	6	---	12	---	18	31	37	---	7
Sclerocarya birrea subsp. *caffra*	26	50	35	60	---	10	---	12	---	18	---	10	---	10	---	6
Aristida stipoides	---	6	---	13	---	10	40	53	---	4	---	18	---	7	---	10
Blepharis obmitrata	---	6	---	20	---	19	---	0	---	10	---	5	---	17	13	24
Erucastrum arabicum	---	6	---	27	---	10	---	0	---	18	---	0	11	23	10	21
Hibiscus calyphyllus	---	6	25	33	---	5	---	0	---	4	---	1	---	14	25	34
Asparagus nelsii	---	11	---	20	32	48	---	0	---	18	---	13	---	7	---	14
Commiphora africana	---	0	24	40	22	38	---	6	---	14	---	6	---	13	---	16
Andropogon chinensis	37	61	---	0	33	57	---	18	---	18	---	6	---	1	---	7
Brachiaria malacodes	---	6	20	33	---	24	---	6	---	12	---	4	---	11	6	20
Digitaria velutina	---	0	26	33	---	0	---	0	---	8	---	4	20	28	---	18
Enteropogon macrostachyus	---	17	---	13	---	10	---	0	---	10	---	8	12	23	---	15
Grewia olukondae	26	33	---	7	---	0	---	3	---	0	24	32	---	14	---	4
Asparagus exuvialis	---	0	---	27	---	10	---	6	---	2	14	23	---	14	---	9
Pentarrhinum insipidum	29	44	---	7	28	43	---	0	---	8	---	1	---	10	---	14
Setaria sagittifolia	---	0	26	33	---	5	---	0	---	2	---	8	34	39	---	3
Bothriochloa radicans	---	0	---	0	---	0	---	3	24	24	---	4	---	10	18	20
Hermannia modesta	---	0	---	7	---	14	21	29	13	22	---	1	---	3	---	14
Chloris virgata	---	0	---	0	---	0	---	3	---	16	---	9	---	10	18	19
Phyllanthus maderaspatensis	---	11	---	7	---	0	---	15	---	4	---	15	---	11	---	11
Gymnema sylvestre	---	17	---	20	---	10	---	3	---	12	---	12	---	13	---	7
Ximenia caffra	14	28	---	27	20	33	---	0	---	2	---	8	---	8	---	11
Spermacoce senensis	---	17	23	33	---	5	---	0	13	24	---	10	---	6	---	7
Euphorbia inaequilatera	---	0	---	0	---	5	---	0	39	37	---	4	---	10	---	11
Aptosimum decumbens	---	0	---	0	---	0	---	3	---	14	15	17	---	1	18	18
Megalochlamys marlothii	---	0	---	0	---	0	---	0	---	18	---	1	---	11	24	22
Solanum delagoense	---	11	---	7	---	14	---	0	---	12	---	5	---	3	16	21

5.1.1.1 Lanneo discoloris-Kirkietum acuminatae ass. nov.

Number of relevés: 18
Number of species observed: 149
Estimated number of species: 259
Average species density in 1000 m^2: 41
Type relevé: 7943 (holotypus), sampled on 15 February 2008 at 19.45389°S, 17.66972°E (Mosbach)
Kirkia acuminata (t2) 10%, *Lannea discolor* (t2) 10%, *Spirostachys africana* (t2) 5%, *Sclerocarya birrea* subsp. *caffra* (t2) 0.5%, *Combretum apiculatum* subsp. *leutweinii* (t3) 5%, *Dichrostachys cinerea* (t3) 5%, *Peltophorum africanum* (t3) 5%, *Spirostachys africana* (t3) 5%, *Commiphora glandulosa* (t3) 1%, *Commiphora tenuipetiolata* (t3) 0.5%, *Croton gratissimus* var. *subgratissimus* (s1) 10%, *Flueggea virosa* (s1) 5%, *Grewia flavescens* (s1) 5%, *Dombeya rotundifolia* (s1) 2%, *Mundulea sericea* (s1) 1%, *Ximenia americana* (s1) 1%, *Cissus nymphaeifolia* (s1) 0.5%, *Commiphora glaucescens* (s1) 0.5%, *Euphorbia guerichiana* (s1) 0.5%, *Ozoroa insignis* (s1) 0.5%, *Terminalia sericea* (s1) 0.5%, *Vachellia nilotica* (s1) 0.5%, *Vangueria infausta* (s1) 0.5%, *Ximenia caffra* (s1) 0.5%, *Cyphostemma congestum* (s2) 0.5%, *Grewia villosa* (s2) 0.5%, *Securidaca longepedunculata* (s2) 0.5%, *Panicum maximum* (gp) 20%, *Digitaria seriata* (gp) 5%, *Heteropogon contortus* (gp) 1%, *Cenchrus ciliaris* (gp) 0.5%, *Enneapogon scoparius* (gp) 0.5%, *Enteropogon macrostachyus* (gp) 0.5%, *Eragrostis lehmanniana* (gp) 0.5%, *Eustachys paspaloides* (gp) 0.5%, *Danthoniopsis dinteri* (ga) 10%, *Brachiaria deflexa* (ga) 0.5%, *Enneapogon cenchroides* (ga) 0.5%, *Melinis repens* subsp. *grandiflora* (ga) 0.5%, *Tephrosia purpurea* (ga) 0.5%, *Cheilanthes marlothii* (hl) 2%, *Hypoestes forskaolii* (hl) 2%, *Bidens biternata* (hl) 1%, *Cheilanthes dinteri* (hl) 1%, *Cleome monophylla* (hl) 1%, *Pellaea calomelanos* (hl) 1%, *Abutilon angulatum* (hl) 0.5%, *Acalypha segetalis* (hl) 0.5%,

Cardiospermum corindum (hl) 0.5%, *Cheilanthes involuta* (hl) 0.5%, *Commelina benghalensis* (hl) 0.5%, *Erucastrum arabicum* (hl) 0.5%, *Hibiscus calyphyllus* (hl) 0.5%, *Hibiscus castroi* (hl) 0.5%, *Kyllinga alba* (hl) 0.5%, *Momordica balsamina* (hl) 0.5%, *Ocimum filamentosum* (hl) 0.5%, *Oxalis purpurascens* (hl) 0.5%, *Pavonia burchellii* (hl) 0.5%, *Pentarrhinum insipidum* (hl) 0.5%, *Phyllanthus pentandrus* (hl) 0.5%, *Pupalia lappacea* (hl) 0.5%, *Rhynchosia venulosa* (hl) 0.5%, *Solanum lichtensteinii* (hl) 0.5%, *Talinum caffrum* (hl) 0.5%, *Tragia okanyua* (hl) 0.5%

Diagnostic species: *Vangueria infausta, Pellaea calomelanos, Cheilanthes dinteri,* *Lannea discolor*, *Cleome monophylla*, *Kirkia acuminata*, *Macrotyloma axillare*, *Commiphora glaucescens*, *Ozoroa insignis*, *Andropogon gayanus* var. *polycladus*, *Merremia pinnata*, *Thunbergia aurea*, *Danthoniopsis dinteri*, *Ipomoea verbascoidea*

Constant species: *Croton gratissimus, Combretum apiculatum, Melinis repens* subsp. *grandiflora,* *Dichrostachys cinerea*, *Dombeya rotundifolia*, *Bidens biternata*, *Ximenia americana*, *Andropogon chinensis*

The *Lanneo discoloris-Kirkietum acuminatae* forms a tall, sub-continuous thicket dominated by the phanerophytes *Kirkia acuminata*, *Croton gratissimus*, *Combretum apiculatum*, *Commiphora glaucescens* and *Lannea discolor.* The grass sward consists of *Danthoniopsis dinteri*, *Panicum maximum*, *Melinis repens* subsp. *grandiflora*, *Eragrostis porosa*, *Digitaria seriata* and *Aristida adscensionis* (Figures 12a, 13a).

The association occurs on moderately steep to steep mountain slopes, mostly of the Nosib Group and Abenab Subgroup type rocks (i.e. quarzites, dolomites, limestone, conglomerate). Large stones (20–60 cm) cover between 15 and 40% of the soil surface, whilst rocks (i.e. bigger than 60 cm) cover between 40 and 80%, sometimes even more. The soils are shallow (<30 cm deep) and medium-textured (Coetzee et al. 1998). The *Lanneo discoloris-Kirkietum acuminatae* occurs at altitudes of between 1290 and 1830 m a.s.l.

5.1.1.2 Commiphoro glaucescentis-Kirkietum acuminatae ass. nov.

Number of relevés: 15
Number of species observed: 156
Estimated number of species: 285
Average species density in 1000 m^2: 44
Type relevé: 8018 (holotypus), sampled on 14 March 2008 at 19.46250°S, 16.90139°E (Olifantspoor)
Kirkia acuminata (t1) 20%, *Sclerocarya birrea* subsp. *caffra* (t1) 1%, *Berchemia discolor* (t2) 10%, *Terminalia prunioides* (t2) 10%, *Commiphora mollis* (t2) 1%, *Commiphora glaucescens* (t3) 10%, *Commiphora mollis* (t3) 10%, *Combretum apiculatum* subsp. *apiculatum* (s1) 10%, *Senegalia erubescens* (s1) 10%, *Flueggea virosa* (s1) 5%, *Grewia bicolor* (s1) 2%, *Cissus nymphaeifolia* (s1) 1%, *Steganotaenia araliacea* var. *araliacea* (s2) 0.5%, *Triraphis ramosissima* (gp) 1%, *Danthoniopsis dinteri* (ga) 5%, *Brachiaria deflexa* (ga) 2%, *Melinis repens* subsp. *grandiflora* (ga) 2%, *Dactyloctenium aegyptium* (ga) 1%, *Eragrostis porosa* (ga) 1%, *Setaria sagittifolia* (ga) 0.5%, *Achyranthes aspera* var. *sicula* (hl) 10%, *Commelina benghalensis* (hl) 10%, *Bidens biternata* (hl) 5%, *Momordica humilis* (hl) 5%, *Acalypha ciliata* (hl) 1%, *Abutilon angulatum* (hl) 0.5%, *Actiniopteris radiata* (hl) 0.5%, *Cleome angustifolia* subsp. *diandra* (hl) 0.5%, *Corchorus tridens* (hl) 0.5%, *Crassocephalum coeruleum* (hl) 0.5%, *Gisekia africana* (hl) 0.5%, *Hibiscus elliottiae* (hl) 0.5%, *Ipomoea dichroa* (hl) 0.5%, *Neorautanenia mitis* (hl) 0.5%, *Phyllanthus pentandrus* (hl) 0.5%, *Rhynchosia totta* (hl) 0.5%, *Schkuhria pinnata* (hl) 0.5%, *Spermacoce senensis* (hl) 0.5%, *Thunbergia aurea* (hl) 0.5%

Diagnostic species: *Danthoniopsis dinteri,* *Cissus nymphaeifolia*, *Steganotaenia araliacea* var. *araliacea*, *Kirkia acuminata*, *Ficus cordata*, *Crassocephalum coeruleum*, *Actiniopteris radiata*, *Berchemia discolor*, *Triraphis ramosissima*, *Momordica humilis*

Constant species: *Croton gratissimus, Combretum apiculatum,* *Terminalia prunioides*, *Melinis repens* subsp. *grandiflora*, *Bidens biternata*, *Grewia flavescens*, *Grewia bicolor*, *Dichrostachys cinerea*, *Commiphora glaucescens*, *Commiphora glandulosa*, *Brachiaria deflexa*

The *Commiphoro glaucescentis-Kirkietum acuminatae* forms a tall, sub-continuous thicket, dominated by the phanerophytes *Kirkia acuminata*, *Commiphora glaucescens*, *Gyrocarpus americanus* subsp. *africanus*, *Croton gratissimus* and *Commiphora mollis.* The grass sward is less diverse, with *Danthoniopsis dinteri* and *Brachiaria malacodes* dominating. *Plectranthus cylindraceus* (a leaf-succulent suffrutex) is also common (Figures 12b, 13b).

This association occurs on steep to very steep mountain slopes, mostly of the Tsumeb Subgroup rocks (mostly dolomites). Stone and rock cover is equally high as with the *Lanneo discoloris-Kirkietum acuminatae*, however more medium-sized stones (5 – 20 cm) are present. The association occurs at altitudes between 1250 and 1640 m a.s.l.

5.1.1.3 Commiphoro glaucescentis-Combretetum apiculati ass. nov.

Number of relevés: 21
Number of species observed: 131
Estimated number of species: 225
Average species density in 1000 m^2: 40
Type relevé: 7910 (holotypus), sampled on 12 February 2008 at 19.54833°S, 17.46556°E (Ma Foi)
Ficus burkei (t2) 1%, *Commiphora glaucescens* (t3) 10%, *Combretum apiculatum* subsp. *apiculatum* (s1) 10%, *Dichrostachys cinerea* (s1) 10%, *Senegalia mellifera* subsp. *detinens* (s1) 10%, *Terminalia prunioides* (s1) 10%, *Croton gratissimus* var. *subgratissimus* (s1) 5%, *Dombeya rotundifolia* (s1) 5%, *Elephantorrhiza suffruticosa* (s1) 5%, *Grewia flava* (s1) 1%, *Commiphora africana* (s1) 0.5%, *Flueggea virosa* (s1) 0.5%, *Gymnosporia senegalensis* (s1) 0.5%, *Lantana angolensis* (s1) 0.5%, *Searsia marlothii* (s1) 0.5%, *Ziziphus mucronata* (s1) 0.5%, *Cissus nymphaeifolia* (s1) 0.1%, *Aerva leucura* (s2) 0.5%, *Mundulea sericea* (s2) 0.5%, *Ehretia rigida* (s2) 0.1%, *Grewia bicolor* (s2) 0.1%, *Eragrostis nindensis* (gp) 5%, *Eragrostis lehmanniana* var. *lehmanniana* (gp) 2%, *Andropogon chinensis* (gp) 0.5%, *Heteropogon contortus* (gp) 0.5%, *Oropetium capense* (gp) 0.5%, *Melinis repens* subsp. *grandiflora*

(ga) 0.5%, *Actiniopteris radiata* (hl) 2%, *Cyperus cuspidatus* (hl) 1%, *Bidens biternata* (hl) 0.5%, *Cheilanthes marlothii* (hl) 0.5%, *Clerodendrum ternatum* (hl) 0.5%, *Dipcadi glaucum* (hl) 0.5%, *Hibiscus caesius* (hl) 0.5%, *Ophioglossum polyphyllum* (hl) 0.5%, *Pavonia burchellii* (hl) 0.5%, *Pentarrhinum insipidum* (hl) 0.5%, *Phyllanthus pentandrus* (hl) 0.5%, *Rhynchosia venulosa* (hl) 0.5%, *Scadoxus multiflorus* (hl) 0.5%, *Eriospermum flagelliforme* (hl) 0.1%, *Gloriosa superba* (hl) 0.1%, *Enneapogon scoparius* (gp) 10%, *Fingerhuthia africana* (gp) 10%, *Anthephora pubescens* (gp) 5%

Diagnostic species: *Fingerhuthia africana*, *Searsia marlothii*, *Commiphora glaucescens*, *Dombeya rotundifolia*, *Anthephora pubescens*, *Eragrostis nindensis*, *Heteropogon contortus*, *Ophioglossum polyphyllum*

Constant species: ***Croton gratissimus, Combretum apiculatum,*** *Terminalia prunioides*, *Mundulea sericea*, *Dichrostachys cinerea*, *Senegalia mellifera* subsp. *detinens*, *Euclea undulata*, *Commiphora glandulosa*

The *Commiphoro glaucescentis-Combretetum apiculati* forms a short, moderately closed thicket dominated by the phanerophytes *Terminalia prunioides*, *Croton gratissimus*, *Commiphora glaucescens*, *Spirostachys africana*, *Kirkia acuminata*, *Dombeya rotundifolia*, *Dichrostachys cinerea* and *Combretum apiculatum*. *Opuntia ficus-indica* has been found to be a common invader in this association. The grass sward is best developed of the three mountain associations, being dominated by *Eragrostis nindensis*, *Enneapogon scoparius*, *Heteropogon contortus*, *Eragrostis scopelophila* and *Enneapogon desvauxii* (Figures 12c, 13c).

This association is occurring on low hills and ridges as well as on mountain peaks, at a wide range of altitudes, between 1440 and 2020 m a.s.l., and on both the Abenab and Tsumeb Subgroups. The habitat is however less steep, being rolling to moderately steep. The substrate is also more fragmented, with gravel (0.2–2 cm) and small stones (2–5 cm) and medium stones prominently occurring on the soil surface (2%, 5% and up to 15%, respectively). Large stones and rocks cover about 40% of the soil surface. The soils are equally shallow as with the other mountain habitats.

5.2 *Terminalietalia prunioidis* ord. nov.

Number of relevés: 329
Type: *Dichrostachyo cinereae-Terminalion prunioidis* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 412
Diagnostic species: *Aristida rhiniochloa*, *Urochloa brachyura*, *Combretum hereroense*, *Senegalia mellifera* subsp. *detinens*, *Terminalia prunioides*
Constant species: ***Dichrostachys cinerea,*** *Grewia bicolor*, *Combretum apiculatum*, *Commiphora glandulosa*, *Melinis repens* subsp. *grandiflora*, *Croton gratissimus*, *Spirostachys africana*, *Grewia flavescens*, *Vachellia nilotica*, *Combretum imberbe*, *Vachellia reficiens / luederitzii*

The *Terminalietalia prunioidis* are subdivided into three groups, of which the latter two are recognised as alliances. The *Dichrostachyo cinereae-Terminalion prunioidis* is designated as the type for this order. The *Terminalietalia prunioidis* represent the Karstveld plains to the north of the Otavi Mountain Range. The first group is characterised by the occurrence of *Anthephora schinzii* together with *Terminalia prunioides*, *Commiphora glandulosa*, *Combretum apiculatum* and *Melinis repens* subsp. *grandiflora*. Two associations have been classified into this group. However, as the composition and habitats of these two groups vary widely, they cannot be grouped into an alliance.

5.2.1.1 Trago pedunculati-Ipomoeetum adenioidis ass. nov.

Number of relevés: 34
Number of species observed: 75
Estimated number of species: 176
Average species density in 1000 m^2: 26
Type relevé: 2794 (holotypus), sampled on 3 April 2003 at 19.25611°S, 18.48389°E (Baden)
Terminalia prunioides (t3) 2%, *Terminalia prunioides* (s1) 10%, *Combretum apiculatum* subsp. *apiculatum* (s1) 2%, *Senegalia mellifera* subsp. *detinens* (s1) 2%, *Combretum hereroense* (s1) 1%, *Croton gratissimus* var. *gratissimus* (s1) 1%, *Grewia bicolor* (s1) 1%, *Pavetta zeyheri* (s1) 1%, *Rhigozum brevispinosum* (s1) 1%, *Ipomoea adenioides* (s2) 2%, *Mundulea sericea* (s2) 2%, *Stipagrostis uniplumis* var. *uniplumis* (gp) 2%, *Eragrostis echinochloidea* (gp) 1%, *Oropetium capense* (gp) 1%, *Anthephora schinzii* (ga) 5%, *Aristida adscensionis* (ga) 1%, *Eragrostis porosa* (ga) 1%, *Melinis repens* subsp. *grandiflora* (ga) 1%, *Tragus pedunculatus* (ga) 1%, *Gisekia africana* (hl) 1%, *Hermannia modesta* (hl) 1%, *Phyllanthus maderaspatensis* (hl) 1%, *Tephrosia dregeana* var. *dregeana* (hl) 1%

Diagnostic species: ***Anthephora schinzii, Ipomoea adenioides,*** *Tragus pedunculatus*, *Vahlia capensis*, *Pavetta zeyheri*

Constant species: ***Terminalia prunioides, Mundulea sericea, Melinis repens*** **subsp.** ***grandiflora,*** *Commiphora glandulosa*, *Senegalia mellifera* subsp. *detinens*, *Croton gratissimus*, *Combretum apiculatum*, *Combretum hereroense*, *Grewia bicolor*, *Combretum imberbe*

The *Trago pedunculati-Ipomoeetum adenioidis* forms a short, semi-open bushland dominated by *Terminalia prunioides*, *Senegalia mellifera* subsp. *detinens* and *Combretum apiculatum*. The grass sward is relatively sparse, being dominated by *Melinis repens* subsp. *grandiflora*, *Anthephora schinzii*, *Tragus berteronianus*, *Panicum coloratum*, *Eragrostis pilgeriana* and *Eragrostis nindensis* (Figures 12d, 13d).

The habitat of this association is formed by denuded plates of calcrete, often associated with slight depressions, or, e.g. along the B6 trunk road, associated with a slight rise in topography forming a natural dam causing water to accumulate. This results in temporary flooding and water logging during the peak rainy season (Figure 13e). Soils are found only in the crevices between the calcrete blocks (near to 80% stone and rock cover). The shallow water evaporates soon, leaving especially the herbaceous layer without an adequate water supply. Consequently, most of these are short-lived annuals. Notable exceptions are *Panicum coloratum*, which is known to prefer pans and watercourses (i.e. waterlogged soils) (Gibbs Russell et al. 1990), and *Eragrostis nindensis*, which is known to be

a poikilohydric plant (Van der Willigen et al. 2003). The phanerophytes also appear stunted, barely reaching 2 m height. The altitude ranges between 1140 and 1300 m a.s.l.

5.2.1.2 Combreto apiculati-Colophospermetum mopane ass. nov.

Number of relevés: 49
Number of species observed: 190
Estimated number of species: 305
Average species density in 1000 m^2: 41
Type relevé: 8022 (holotypus), sampled on 14 March 2008 at 19.50250°S, 16.93444°E (Derna)
Colophospermum mopane (t1) 5%, *Spirostachys africana* (t2) 1%, *Colophospermum mopane* (t3) 60%, *Terminalia prunioides* (t3) 20%, *Combretum apiculatum* subsp. *apiculatum* (s1) 5%, *Grewia bicolor* (s1) 5%, *Senegalia cinerea* (s1) 5%, *Dichrostachys cinerea* (s1) 2%, *Croton gratissimus* var. *gratissimus* (s1) 1%, *Croton menyharthii* (s1) 1%, *Grewia avellana* (s1) 1%, *Megalochlamys marlothii* (s2) 0.5%, *Bothriochloa radicans* (gp) 2%, *Enteropogon macrostachyus* (gp) 2%, *Enneapogon scoparius* (gp) 0.5%, *Microchloa caffra* (gp) 0.5%, *Aristida rhiniochloa* (ga) 2%, *Eragrostis porosa* (ga) 2%, *Setaria pumila* (ga) 2%, *Aristida effusa* (ga) 1%, *Melinis repens* subsp. *grandiflora* (ga) 1%, *Sporobolus panicoides* (ga) 1%, *Brachiaria deflexa* (ga) 0.5%, *Abutilon austro-africanum* (hl) 0.5%, *Bidens biternata* (hl) 0.5%, *Hibiscus calyphyllus* (hl) 0.5%, *Hibiscus elliottiae* (hl) 0.5%, *Indigastrum parviflorum* (hl) 0.5%, *Ipomoea sinensis* (hl) 0.5%, *Ocimum filamentosum* (hl) 0.5%, *Ruellia prostrata* (hl) 0.5%

Diagnostic species: *Colophospermum mopane*

Constant species: ***Terminalia prunioides, Dichrostachys cinerea, Combretum apiculatum, Commiphora glandulosa, Melinis repens* subsp. *grandiflora,*** *Setaria pumila*, *Urochloa brachyura*, *Grewia bicolor*, *Grewia flavescens*

The *Combreto apiculati-Colophospermetum mopane* forms a short, moderately closed bushland, dominated by the phanerophytes *Terminalia prunioides*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Combretum apiculatum* and *Commiphora glandulosa*. The grass sward consists of *Eragrostis nindensis*, *Setaria pumila*, *Eragrostis porosa*, *Enneapogon desvauxii*, *Urochloa brachyura*, *Enneapogon cenchroides* and *Anthephora schinzii*. The annual herb *Sericorema sericea* and sedges *Cyperus hamulosus* and *Eleocharis atropurpurea* are also conspicuous in this association (Figures 12e, 13f).

Le Roux (Le Roux 1980; Le Roux et al. 1988) describes a 'Thai-tkab veld' and a 'Maroela Association' along the eastern part of the Etosha National Park, bordering the present study area. These veld types are dominated by *Terminalia prunioides*, *Colophospermum mopane*, *Combretum apiculatum* and *Spirostachys africana*. Within the Maroela association, some *Sclerocarya birrea* trees are found. This is essentially the same as the *Combreto apiculati-Colophospermetum mopane* under discussion here. Le Roux describes the soils on rises as shallow leptosols on calcrete boulders, whilst in the depressions 'Arcadia' form soils (i.e. vertisols) are present (Soil Classification Working Group 1991). The topography is generally flat, at an altitudinal range of between 1140 and 1310 m a.s.l..

The occurrence of *Colophospermum mopane* is not restricted to the *Combreto apiculati-Colophospermetum mopane*. The species occurs intermittently within the *Dichrostachyo cinereae-Terminalietum prunioidis* to the west and north-west of Tsumeb, gradually increasing in abundance. Anecdotal evidence has it that the species occurred far more east of its present distribution area, but over-utilisation for construction timber and especially mine props in the Tsumeb Mine during the early previous Century led to the gradual retreat of the species to the west.

5.2.2 Terminalio prunioidis-Hyphaenion petersianae all. nov.

Synopsis:
Number of relevés: 78
Type: *Terminalio prunioidis-Hyphaenetum petersianae* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 216
This alliance consists of a single association, which also serves as its type.

5.2.2.1 Terminalio prunioidis-Hyphaenetum petersianae ass. nov.

Number of relevés: 78
Number of species observed: 216
Estimated number of species: 376
Average species density in 1000 m^2: 40
Type relevé: 2793 (holotypus), sampled on 3 April 2003 at 19.21833°S, 18.52417°E (Elandslaagte)
Hyphaene petersiana (t2) 1%, *Spirostachys africana* (t2) 1%, *Commiphora glandulosa* (t3) 1%, *Terminalia prunioides* (s1) 40%, *Combretum apiculatum* subsp. *apiculatum* (s1) 5%, *Dichrostachys cinerea* (s1) 5%, *Peltophorum africanum* (s1) 5%, *Vachellia nilotica* (s1) 5%, *Grewia bicolor* (s1) 2%, *Hyphaene petersiana* (s1) 2%, *Senegalia mellifera* subsp. *detinens* (s1) 2%, *Albizia anthelmintica* (s1) 1%, *Grewia flava* (s1) 1%, *Ximenia caffra* (s1) 1%, *Ziziphus mucronata* subsp. *mucronata* (s1) 1%, *Aristida congesta* (gp) 1%, *Eragrostis trichophora* (gp) 1%, *Heteropogon contortus* (gp) 1%, *Sporobolus fimbriatus* (gp) 1%, *Stipagrostis uniplumis* var. *uniplumis* (gp) 1%, *Urochloa brachyura* (ga) 5%, *Aristida adscensionis* (ga) 2%, *Aristida effusa* (ga) 2%, *Brachiaria deflexa* (ga) 2%, *Aristida rhiniochloa* (ga) 1%, *Digitaria velutina* (ga) 1%, *Enneapogon cenchroides* (ga) 1%, *Melinis repens* subsp. *grandiflora* (ga) 1%, *Sporobolus panicoides* (ga) 1%, *Tragus racemosus* (ga) 1%, *Pogonarthria fleckii* (ga) 0.1%, *Monechma spartioides* (hl) 5%, *Evolvulus alsinoides* (hl) 1%, *Indigofera charlieriana* (hl) 1%, *Limeum fenestratum* (hl) 1%, *Melhania acuminata* (hl) 1%, *Ocimum americanum* var. *americanum* (hl) 1%, *Otoptera burchellii* (hl) 1%, *Phyllanthus maderaspatensis* (hl) 1%, *Pupalia lappacea* (hl) 1%, *Rhynchosia venulosa* (hl) 1%, *Seddera suffruticosa* (hl) 1%, *Talinum crispatulum* (hl) 1%, *Tephrosia dregeana* var. *dregeana* (hl) 1%

Diagnostic species: *Aristida congesta* subsp. *congesta*, *Hyphaene petersiana*, *Waltheria indica*, *Stipagrostis uniplumis* var. *uniplumis*, *Sporobolus fimbriatus*, *Schmidtia pappophoroides*, *Pogonarthria fleckii*, *Schizachyrium exile*,

Kyphocarpa angustifolia, *Eragrostis rigidior*, *Aristida rhiniochloa*, *Evolvulus alsinoides*

Constant species: *Terminalia prunioides, Combretum apiculatum, Dichrostachys cinerea, Senegalia mellifera* subsp. *detinens, Grewia bicolor, Urochloa brachyura, *Commiphora glandulosa*, *Spirostachys africana*, *Vachellia nilotica*

The *Terminalio prunioidis-Hyphaenetum petersianae* forms a tall, sub-continuous thicket dominated by the phanerophytes *Terminalia prunioides*, *Combretum apiculatum*, *Spirostachys africana*, *Senegalia mellifera* subsp. *detinens*, *Dichrostachys cinerea*, *Vachellia reficiens / luederitzii*, *Vachellia nilotica*, *Hyphaene petersiana*, *Croton gratissimus* and *Commiphora glandulosa*. The grass sward is dominated by *Pogonarthria fleckii*, *Aristida congesta* subsp. *congesta*, *Schizachyrium exile*, *Aristida rhiniochloa*, *Urochloa brachyura*, *Eragrostis trichophora*, *Eragrostis rigidior*, *Cymbopogon caesius*, *Chrysopogon nigritanus* and *Aristida effusa***.** The leaf succulent *Sansevieria pearsonii* is also conspicuous in this association (Figures 12f, 13g).

The *Terminalio prunioidis-Hyphaenetum petersianae* forms a distinct zone between the eastern, north-eastern and southern plains and the adjacent riverine habitats (Omuramba Ovambo and Omuramba Omatako). This is locally referred to as the '*Palmvlakte´* ('palm plains', referring to the presence of the makalani palm, *Hyphaene petersiana*). *Hyphaene petersiana* is known to occur in soils with a shallow water table, e.g. along the fringes of the Oshana system in central-northern Namibia (Fanshawe 1967; Mendelsohn et al. 2000, 2013). Also *Chrysopogon nigritanus* is known to occur in close proximity to wetlands (Gibbs Russell et al. 1990). The soils are generally without stone cover, flat and at an altitudinal range of between 1150 and 1240 m a.s.l.

5.2.3 Dichrostachyo cinereae-Terminalion prunioidis all. nov.

Number of relevés: 169
Type: *Dichrostachyo cinereae-Terminalietum prunioidis* B. Strohbach & M. Strohbach 2023 (see below)
Number of species observed: 316
Constant species: *Dichrostachys cinerea, Terminalia prunioides, Senegalia mellifera* subsp. *detinens, Grewia bicolor, *Combretum apiculatum*, *Urochloa brachyura*, *Vachellia reficiens / luederitzii*, *Croton gratissimus*, *Vachellia nilotica*, *Spirostachys africana*, *Grewia flavescens*, *Brachiaria deflexa*, *Commiphora glandulosa*, *Melinis repens* subsp. *grandiflora*, *Grewia villosa*, *Enneapogon cenchroides*

No diagnostic species were identified.

This order, representing the Karstveld plains to the east, north and west of the Otavi mountain range, are characterised by the constant occurrence of ***Dichrostachys cinerea, Terminalia prunioides, Senegalia mellifera* subsp. *detinens, Grewia bicolor,** *Combretum apiculatum* and *Urochloa brachyura***.** Two associations were identified under this alliance.

5.2.3.1 Terminalio prunioidis-Spirostachyetum africanae le Roux ex B. Strohbach & M. Strohbach ass. nov.

Number of relevés: 71
Number of species observed: 185
Estimated number of species: 356
Average species density in 1000 m^2: 35
Type relevé: 8062 (holotypus), sampled on 17 March 2008 at 18.90972°S, 17.23694°E (Onkoshi)
Spirostachys africana (t2) 10%, *Terminalia prunioides* (t2) 10%, *Vachellia luederitzii* (t3) 5%, *Albizia anthelmintica* (t3) 1%, *Terminalia prunioides* (t3) 1%, *Dichrostachys cinerea* (s1) 10%, *Senegalia mellifera* subsp. *detinens* (s1) 10%, *Terminalia prunioides* (s1) 10%, *Croton gratissimus* var. *subgratissimus* (s1) 5%, *Vachellia nilotica* (s1) 5%, *Grewia bicolor* (s1) 2%, *Grewia villosa* (s1) 2%, *Croton menyharthii* (s2) 10%, *Eragrostis porosa* (ga) 10%, *Enneapogon cenchroides* (ga) 2%, *Brachiaria deflexa* (ga) 1%, *Setaria sagittifolia* (ga) 1%, *Setaria verticillata* (ga) 1%, *Urochloa brachyura* (ga) 1%, *Chloris pycnothrix* (ga) 0.5%, *Digitaria velutina* (ga) 0.5%, *Melinis repens* subsp. *grandiflora* (ga) 0.5%, *Tragus berteronianus* (ga) 0.5%, *Tragus racemosus* (ga) 0.5%, *Erucastrum arabicum* (hl) 5%, *Achyranthes aspera* var. *sicula* (hl) 2%, *Bidens biternata* (hl) 2%, *Acrotome inflata* (hl) 1%, *Limeum sulcatum* (hl) 1%, *Abutilon austro-africanum* (hl) 0.5%, *Acrachne racemosa* (hl) 0.5%, *Cucumis anguria* (hl) 0.5%, *Euphorbia inaequilatera* (hl) 0.5%, *Hibiscus calyphyllus* (hl) 0.5%, *Hibiscus elliottiae* (hl) 0.5%, *Hirpicium gazanioides* (hl) 0.5%, *Ipomoea sinensis* (hl) 0.5%, *Kyphocarpa angustifolia* (hl) 0.5%, *Melhania virescens* (hl) 0.5%

Constant species: ***Dichrostachys cinerea, Terminalia prunioides, Grewia bicolor, Spirostachys africana,** *Senegalia mellifera* subsp. *detinens*, *Urochloa brachyura*, *Brachiaria deflexa*

Le Roux (1980) and Le Roux et al. (1988) described a *Terminalia prunioides-Spirostachys africana* woodland occurring at and south of Namutoni in the Etosha National Park. Here we validate the name according to the ICPN.

The same vegetation, dominated by *Terminalia prunioides*, *Spirostachys africana*, *Dichrostachys cinerea*, *Urochloa brachyura*, *Eragrostis porosa*, *Senegalia mellifera* subsp. *detinens*, *Grewia bicolor*, *Croton gratissimus*, *Brachiaria deflexa*, *Croton menyharthii*, *Vachellia nilotica*, *Kirkia acuminata*, *Hypoestes forskaolii*, *Grewia olukondae*, *Ficus burkei*, *Enneapogon desvauxii*, *Combretum imberbe* and *Combretum apiculatum* occurs widespread as riparian forest in and around the Omuramba Ovambo. In the middle reaches, within the *Parkiesveld* landscape, the *Terminalio prunioidis-Spirostachyetum africanae* form distinct tree islands in the grassland matrix formed by the *Aristido stipoidis-Willkommietum sarmentosae*, often enclosing an ephemeral vley of the *Nymphoides indica-Echinochloa pyramidalis* community (Figures 6c, 7a). The availability of shallow ground water often results in the inclusion of *Sclerocarya birrea* and/or *Adansonia digitata* trees in these forest islands (e.g. at the 'Giant Baobab Tree' Monument on the farm Die Park.) The association forms a tall, sub-continuous thicket (Figures 12g, 13h). The soils are of fluvial origin, often sandy, and generally organically enriched from litter. No stone cover was observed. The topography is flat, at an altitudinal range of between 1150 and 1310 m a.s.l.

5.2.3.2 *Dichrostachyo cinereae-Terminalietum prunioidis* ass. nov.

Number of relevés: 98
Number of species observed: 291
Estimated number of species: 467
Average species density in 1000 m²: 44
Type relevé: 8104 (holotypus), sampled on 16 April 2008 at 19.15389°S, 17.62694°E (Pasadena)
Vachellia luederitzii (t2) 2%, *Terminalia prunioides* (t3) 10%, *Combretum imberbe* (t3) 1%, *Commiphora glandulosa* (t3) 1%, *Commiphora tenuipetiolata* (t3) 1%, *Terminalia prunioides* (s1) 60%, *Dichrostachys cinerea* (s1) 10%, *Combretum apiculatum* subsp. *apiculatum* (s1) 2%, *Croton gratissimus* var. *subgratissimus* (s1) 2%, *Grewia bicolor* (s1) 2%, *Peltophorum africanum* (s1) 2%, *Flueggea virosa* (s1) 1%, *Montinia caryophyllacea* (s1) 1%, *Mundulea sericea* (s1) 1%, *Ozoroa insignis* (s1) 1%, *Vachellia nilotica* (s1) 1%, *Ziziphus mucronata* (s1) 1%, *Spirostachys africana* (s1) 0.5%, *Solanum tettense* var. *renschii* (s2) 5%, *Lantana angolensis* (s2) 1%, *Ehretia alba* (s2) 0.5%, *Megalochlamys marlothii* (s2) 0.5%, *Senegalia mellifera* subsp. *detinens* (s2) 0.5%, *Maerua juncea* (s2) 0.1%, *Cenchrus ciliaris* (gp) 2%, *Heteropogon contortus* (gp) 1%, *Enneapogon scoparius* (gp) 0.5%, *Enteropogon macrostachyus* (gp) 0.5%, *Eragrostis lehmanniana* var. *lehmanniana* (gp) 0.5%, *Eragrostis nindensis* (gp) 0.5%, *Setaria pumila* (ga) 5%, *Sporobolus panicoides* (ga) 2%, *Aristida adscensionis* (ga) 1%, *Eragrostis porosa* (ga) 1%, *Urochloa brachyura* (ga) 1%, *Aristida effusa* (ga) 0.5%, *Aristida rhiniochloa* (ga) 0.5%, *Brachiaria malacodes* (ga) 0.5%, *Enneapogon cenchroides* (ga) 0.5%, *Enneapogon desvauxii* (ga) 0.5%, *Melinis repens* subsp. *grandiflora* (ga) 0.5%, *Setaria verticillata* (ga) 0.5%, *Stipagrostis hirtigluma* subsp. *hirtigluma* (ga) 0.5%, *Tragus racemosus* (ga) 0.5%, *Rhynchosia minima* (hl) 5%, *Kohautia aspera* (hl) 2%, *Melhania virescens* (hl) 2%, *Sericorema sericea* (hl) 2%, *Abutilon austro-africanum* (hl) 1%, *Acrotome inflata* (hl) 1%, *Bidens biternata* (hl) 1%, *Blepharis leendertziae* (hl) 1%, *Erucastrum arabicum* (hl) 1%, *Calostephane divaricata* (hl) 0.5%, *Eriospermum flagelliforme* (hl) 0.5%, *Euphorbia inaequilatera* (hl) 0.5%, *Hermannia modesta* (hl) 0.5%, *Hibiscus caesius* (hl) 0.5%, *Hirpicium gazanioides* (hl) 0.5%, *Ipomoea sinensis* (hl) 0.5%, *Melhania acuminata* (hl) 0.5%, *Otoptera burchellii* (hl) 0.5%, *Polygala albida* subsp. *albida* (hl) 0.5%, *Seddera suffruticosa* (hl) 0.5%, *Solanum delagoense* (hl) 0.5%, *Tephrosia dregeana* var. *dregeana* (hl) 0.5%

Diagnostic species: none

Constant species: *Dichrostachys cinerea, Terminalia prunioides, Senegalia mellifera* subsp. *detinens,* *Grewia bicolor*, *Combretum apiculatum*, *Vachellia reficiens / luederitzii*, *Croton gratissimus*

The *Dichrostachyo cinereae-Terminalietum prunioidis* forms a short, sub-continuous thicket dominated by the phanerophytes *Terminalia prunioides*, *Dichrostachys cinerea*, *Senegalia mellifera* subsp. *detinens*, *Vachellia reficiens / luederitzii* and *Croton gratissimus.* The grass sward is not well developed and dominated by few perennial and mostly annual species: *Enneapogon desvauxii*, *Urochloa brachyura*, *Eragrostis porosa*, *Setaria pumila*, *Heteropogon contortus*, *Enteropogon macrostachyus*, *Pogonarthria fleckii* and *Aristida adscensionis* (Figures 12h, 13i). Bush encroachment is a serious threat to this association.

Initial classification results indicated a potential subdivision into three subunits, however the composition differences suggest rather observer and seasonal bias. For this reason, the three subunits have been combined as one.

This association occurs widespread on the plains north, east and west of the Otavi mountain range, often also in the valleys between these mountains. Several relevés have been classified into this association south of the Otavi mountain range, in a mosaic with the *Cenchro ciliaris-Senegalietum detinentis* and the *Eucleo undulatae-Oleetum africanae*, emphasising the transitional nature of the northern Thornshrub savanna. The soils are typical mollic Leptosols or leptic Regosols on shallow calcrete. Stone cover varies between 5 and 15% cover, with a general mixture of small, medium and large stones. The landscapes are flat to gently undulating, ranging between 1140 and 1600 m a.s.l.

Biodiversity indices

According to the observed species richness (alpha diversity), the community types fall into three groups (Figure 14a): The wetland associations (1.1 and 1.2) and the habitat-wise closely related *Sporobolus-Odyssea paucinervis* association (2.1.1) have the lowest number of species. Of intermediate richness are the three grassland types (2.1.2, 2.2.1 and 2.2.2) as well as the *Terminalio sericeae-Schinziophyetum rautanenii* (4.1) and the *Trago pedunculati-Ipomoeetum adenioidis* (5.2.1). The lower species richness of the *Aristido stipoidis-Willkommietum sarmentosae* and *Trago pedunculati-Ipomoeetum adenioidis* is easily explained by the harsh habitat provided by the shallow soils combined with water logging during the rainy season. All other savanna types display a variable, but generally high species richness.

The gamma diversity indicated similar trends as the species richness (Figure 14b). In many cases the estimated number of species was significantly higher than the observed number. This can be an indicator for both a high internal variability within the associations and possibly also a general undersampling.

According to the Simpson's Index, the three wetland types (including the *Sporobolo-Odysseetum paucinervis*) (1.1, 1.2 and 2.1.1) show a relatively lower degree of dominance (Figure 14c). All other associations are dominated by few species, whilst most species occur with relatively low cover. Of note is the high dominance associated with low variability of the *Terminalio sericeae-Schinziophyetum rautanenii* (4.1). This could be a result of a few large trees (either *Schinziophyton rautanenii* or *Pterocarpus angolensis*) dominating and overshading the stand, resulting also in a lower number of species observed in the association (Figure 14a). This trend is also confirmed by a greater evenness score of the Smith-Wilson Index for this association (Figure 14d).

Environmental drivers

The NMS produced an ordination in three dimensions, with the final stress for the best solution being 19.6%, and

a final instability of 0.00000, after 118 iterations. The randomised data in the Monte Carlo test did not result in a stable solution after 249 iterations. The ordination graph is presented in Figure 15. The tree main vegetation types, Thornbush – Karst transition, Kalahari and the *Terminalietea prunioidis* are moderately well separated. Especially the *Terminalietea prunioidis* and the Thornbush – Karst transition vegetation are indistinguishable on Axis 3. The main environmental drivers, as determined by biplots, were soil depth (r = -0.457) for Axis 1, sandiness (r = -0.332), slope (r = 0.338), rock cover (r = 0.356) and mean annual precipitation (r = 0.348) for Axis 2, as well as gravel cover (r = -0.508) and small stone cover (r = -0.331) for Axis 3. The relatively low correlations necessitated reducing the joint plot cutoff level to r^2 = 0.100 as compared to the default value for r^2 = 0.200.

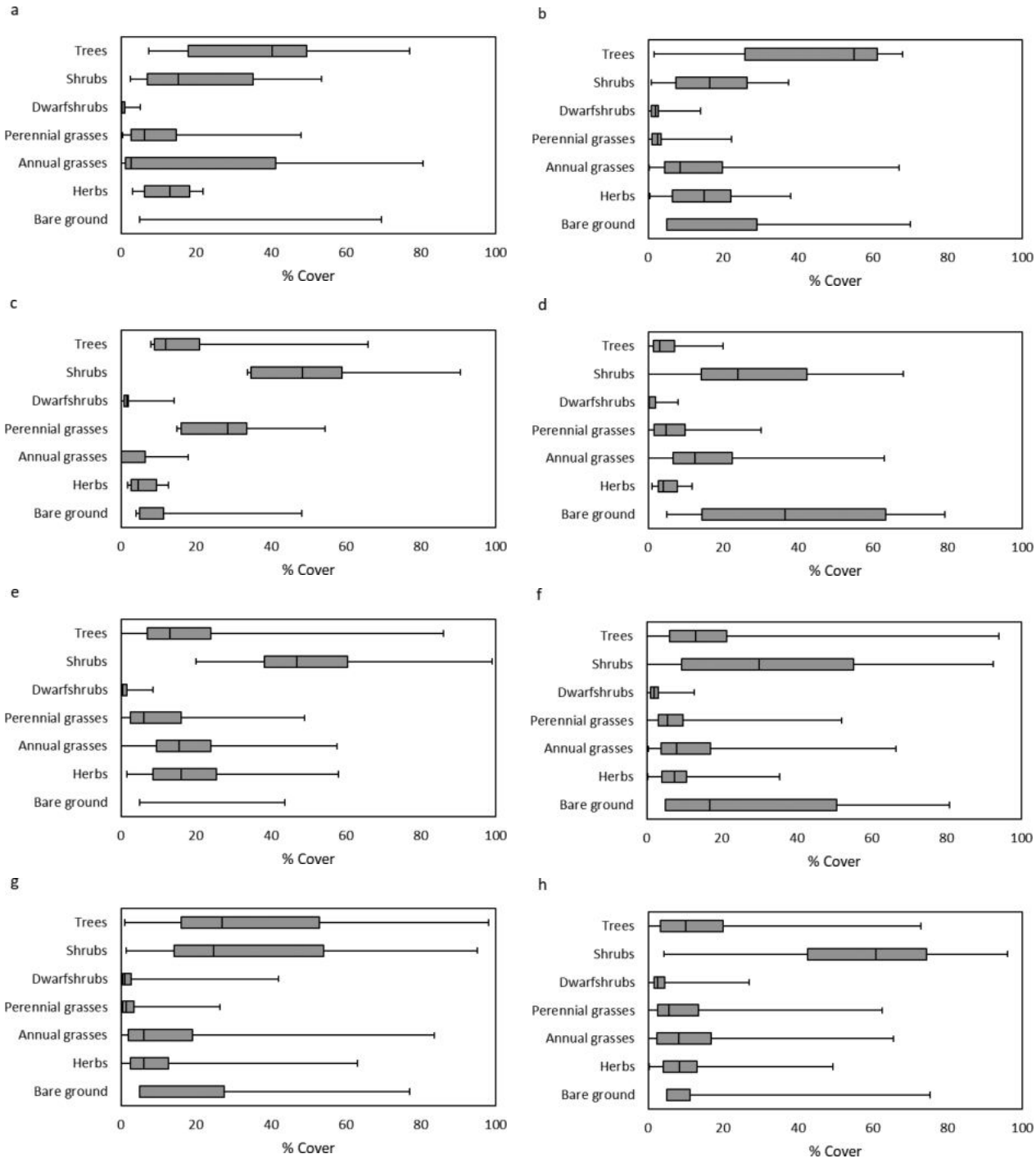

Figure 12. Typical structure of the associations of the *Terminalietea prunioidis*: (**a**) *Lanneo discoloris-Kirkietum acuminatae*; (**b**) *Commiphoro glaucescentis-Kirkietum acuminatae*; (**c**) *Commiphoro glaucescentis-Combretetum apiculati*; (**d**) *Trago pedunculati-Ipomoeetum adenioidis*; (**e**) *Combreto apiculati-Colophospermetum mopane*; (**f**) *Terminalio prunioidis-Hyphaenetum petersianae*; (**g**) *Terminalio prunioidis-Spirostachyetum africanae*; (**h**) *Dichrostachyo cinereae-Terminalietum prunioidis*.

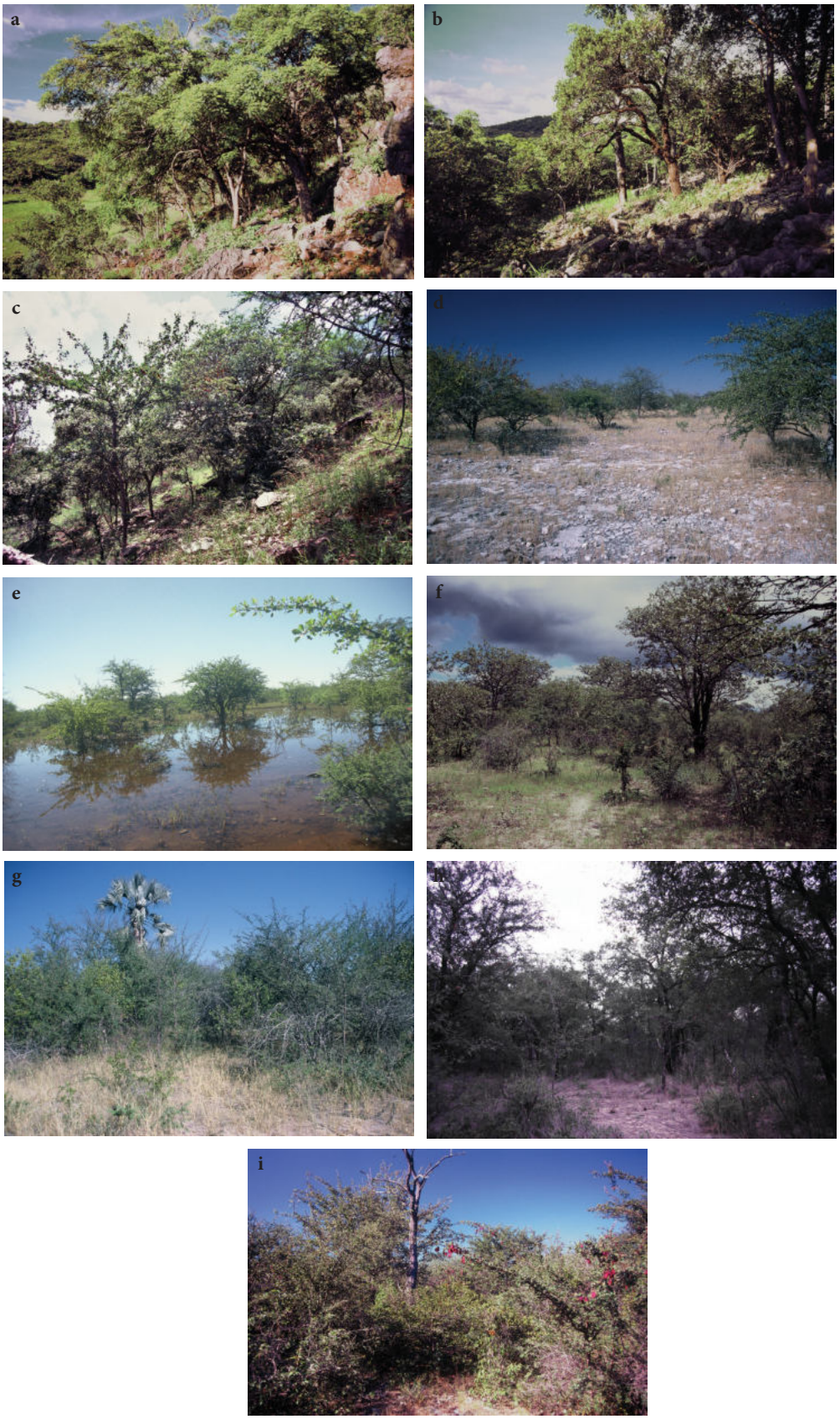

Figure 13. Typical views of the associations of the *Terminalietea prunioidis*: (**a**) *Lanneo discoloris-Kirkietum acuminatae*, relevé 7951; (**b**) *Commiphoro glaucescentis-Kirkietum acuminatae*, relevé 7934; (**c**) *Commiphoro glaucescentis-Combretetum apiculati*, relevé 7971; (**d**) *Trago pedunculati-Ipomoeetum adenioidis*, relevé 2794; (**e**) *Trago pedunculati-Ipomoeetum adenioidis* during the peak rainy season; (**f**) *Combreto apiculati-Colophospermetum mopane*, relevé 8071; (**g**) *Terminalio prunioidis-Hyphaenetum petersianae*, relevé 2793; (**h**) *Terminalio prunioidis-Spirostachyetum africanae*, relevé 7771; (**i**) *Dichrostachyo cinereae-Terminalietum prunioidis*, relevé 8113.

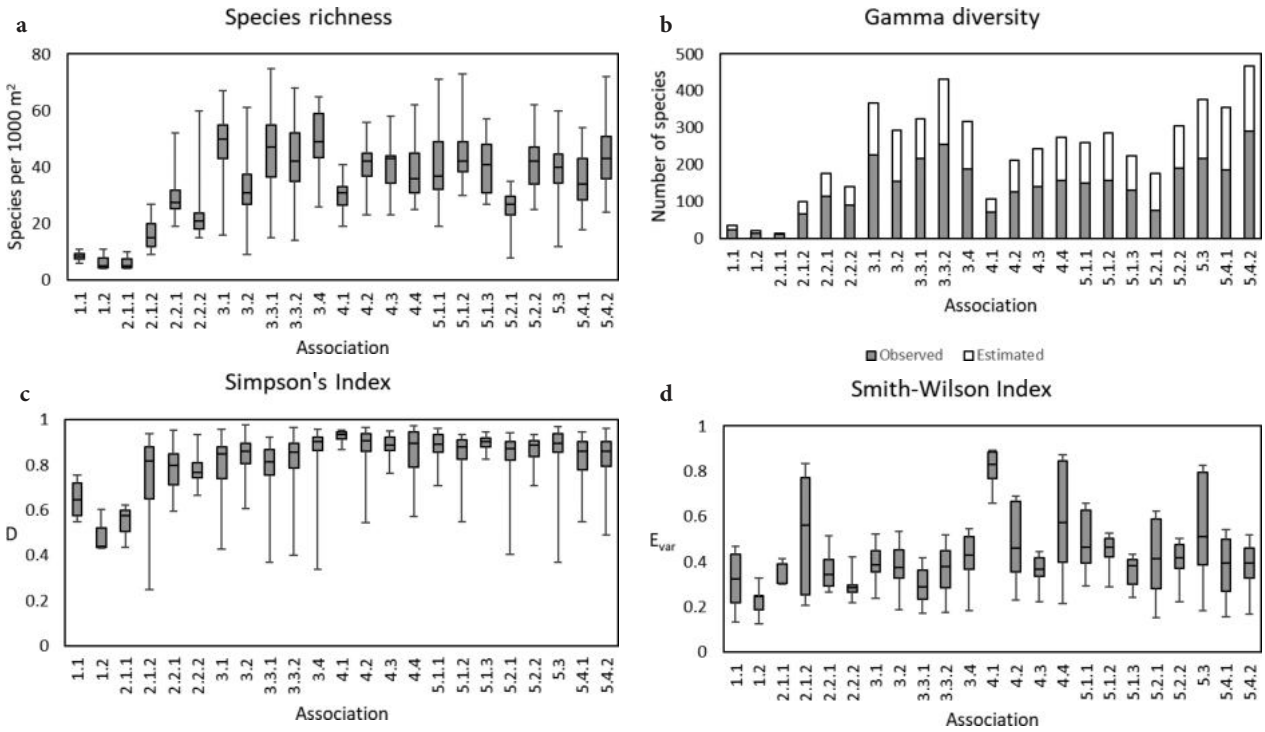

Figure 14. Biodiversity indicators for the various associations described above. (**a**) Species richness per relevé sampled on 1000 m²; (**b**) Gamma diversity for the various associations, indicating both observed and estimated number of species; (**c**) Simpson's Index (D) indicating dominance; (**d**) Smith-Wilson Index (E_{var}) indicating evenness.

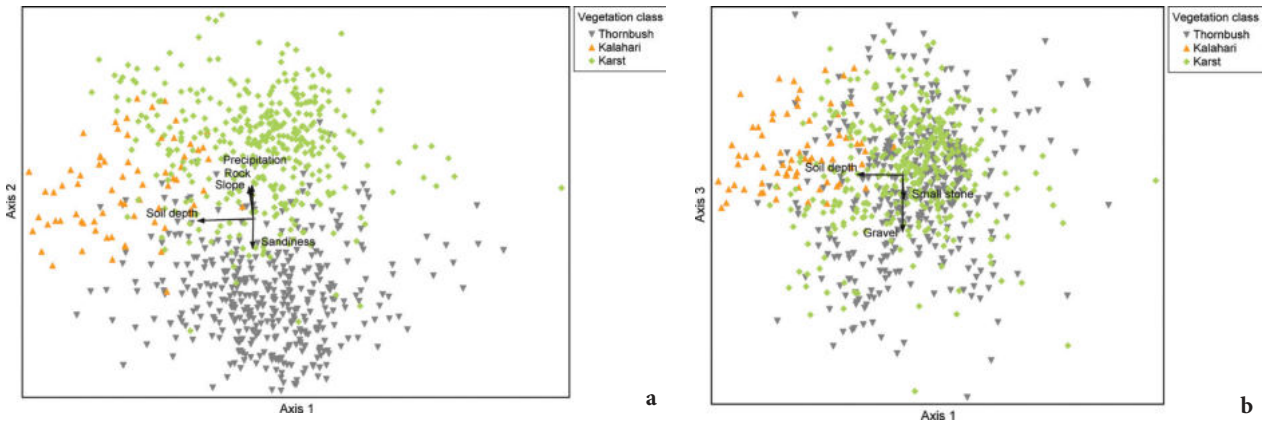

Figure 15. NMS ordination diagrams for the three savanna vegetation types, being the Thornbush – Karst transition, the Kalahari and the *Terminalietea prunioidis*. Top: Axis 1 against Axis 2; bottom Axis 1 against Axis 3.

From the ordination diagrams it is clear that the Kalahari types favour deep soils, the Thornbush – Karstveld transition types the more sandy soils towards the southern study area, whilst the *Terminalietea prunioidis* associations are concentrated on mollic soils and/or stony to rocky soils. This is confirmed by the species distribution of some of the characteris phanerophytic species (Figure 16): Typically, *Terminalia sericea*, *Combretum collinum* and *Vachellia erioloba* favour deep, sandy soils, whilst *Senegalia mellifera* subsp. *detinens* and *Olea europea* subsp. *africana* prefer the more sandy, not necessarily deep soils south of the Karstveld. *Spirostachys africana* and *Terminalia prunioides* prefer shallow loamy to clayey (mollic) soils, whilst *Kirkia acuminata* and *Commiphora glaucescens* clearly prefer steep, rocky habitats, however often associated with deepish (> 50 cm) soil pockets amongst the rocks. As major encroaching species, *Dichrostachys cinerea* shows no particular preference for any habitat. As the environmental variables used in this modelling are qualitative rather than empirically measured, these trends are also to be seen as indicative rather than predictive.

To illustrate the distribution of associations within the landscape, classified relevés within two 30 km wide transects (see Figure 2) were selected and graphed against the position and topography. These graphic representation of the distribution of vegetation associations are presented in Figure 17. The high degree of mosaicking especially within the Otavi mountain range and along the Omuramba Ovambo is clearly illustrated.

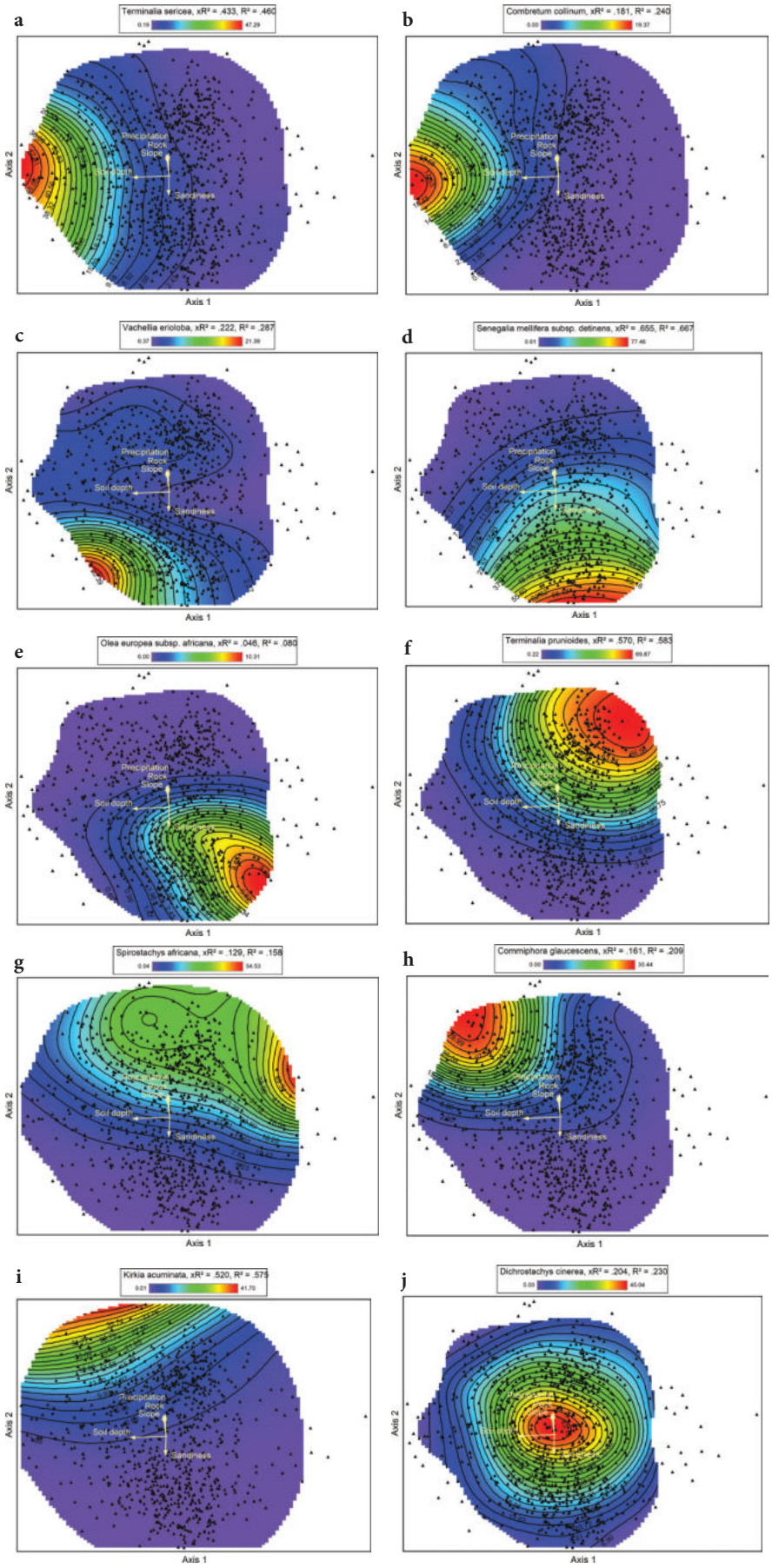

Figure 16. Selected species' response to the main environmental drivers in the Karstveld.

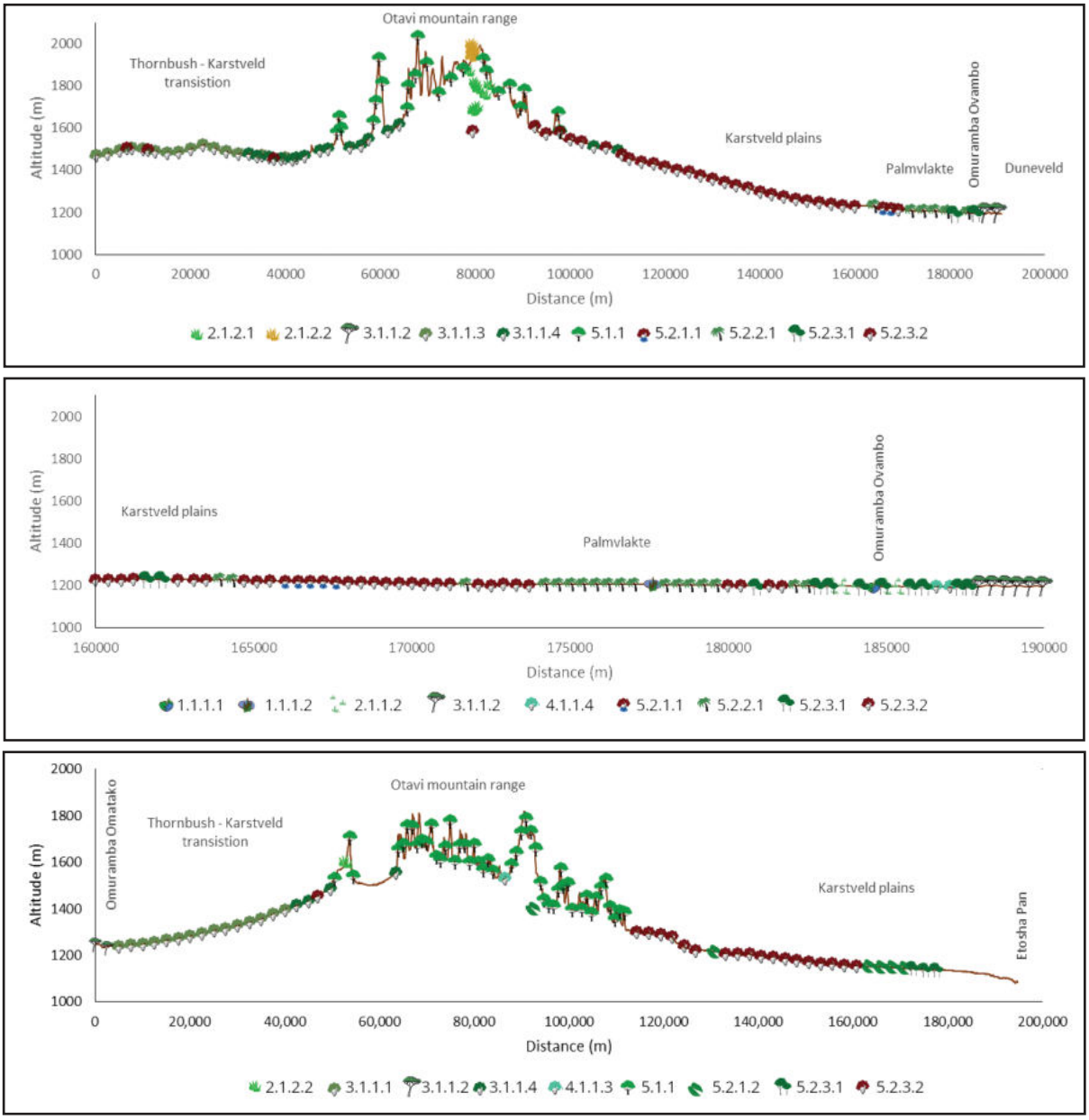

Figure 17. Schematic representation of the main vegetation associations across the topographic gradients represented by the transects in Figure 2. The altitude (*y*-axis) has been exaggerated for visualisation purposes, i.e. is not to scale. (**a**) Transect 1 from SW to NE. (**b**) Detail of the last 30 km of transect 1 (NE point), to show details regarding the mosaicking of vegetation associations around the Omuramba Ovambo. (**c**) Transect 2 from SE to NW. Note the Hoab Valley (ca 60 km from the start of the transect) is completely cleared and tilled for crop production, thus no associations are indicated there.

Conclusions

With this paper, we formally describe 17 new associations with two new subassociations within a major landscape, the Karstveld *sensu* Giess (1998) in north-central Namibia. Large parts of this landscape belong to the newly described *Terminaletea prunioidis*. All associations are clearly defined by way of diagnostic species (see Tables 2–5), yet there is a high variability in the composition of the associations. This is evident especially within the *Terminalio prunioidis-Hyphaenetum petersianae*, *Terminalio prunioidis-Spirostachyetum africanae* and *Dichrostachyo cinereae-Terminalietum prunioidis*. Elements of the *Combreto apiculati-Colophospermetum mopane* have been found with the *Dichrostachyo cinereae-Terminalietum prunioidis*; whilst elements of the *Dichrostachyo cinereae-Terminalietum prunioidis* have been found within the *Cenchro ciliaris-Senegalietum detinentis*. These mosaicking trends are also clearly illustrated by the NMS results (Figure 15).

With continued review of available data and unpublished reports (e.g. Le Roux 1980; Viljoen 1980; Becker 2001; Marufu 2023), further associations and communities belonging to the also newly described *Commpihoro glaucentis-Kirkietalia acuminata* will be identified and described in especialy

the Kunene Region of north-western Namibia, as here an generaly overlooked, but important extension of the Otavi Group carbonate rocks is situated (South African Committee for Stratigraphy 1980; Miller 1997; Giess 1998). There are also indications that the vegetation of the Aha Hills in far-eastern Otjozondjupa Region, Namibia, and possibly the Tsodilo Hills, north-western Botswana, could be part of this order (Hines 1992; Wendorff 2005). Likewise, the newly described *Terminalietalia prunioidis* has outliers in the northern Oshikoto region, beyond the present study area, the Naye-Naye area of easter Otjozondjupa region as well as between Ghanzi and Maun in north-western Botswana (Cole and Brown 1976; Hines 1992; Strohbach 2000, 2014). In how far this order overlaps or can be separated from the Mopane Savanna *sensu* Giess (1998) to the west (as *Terminalia prunioides* is in vast parts co-dominant with *Colophospermum mopane*), will only be revealed by further reviews (Le Roux 1980; Viljoen 1980; Le Roux et al. 1988; Giess 1998; Becker 2001; Du Plessis 2001; Siebert et al. 2003; Marufu 2023).

The higher syntaxonomic divisions of the described associations of the Kalahari, Thornbush – Karstveld transistion and wetlands and grasslands remains even more speculative. For the Kalahari vegetation, a good start has been made with the description of the vegetation in the eastern Otjozondjupa and Omaheke Regions (Strohbach 2014), however, this landscape extends throughout large parts of central Botswana into north-westen South Africa as part of the Kalahari *Acacia-Baikiaea* woodlands ecoregion (Olson et al. 2001; Spriggs 2001b). Also, the differentiation from this ecoregion to the Zambezian *Baikiaea* woodlands ecoregion (Olson et al. 2001; Vetter 2001) is yet to be determined, as this forms a very gradual transition according to increasing rainfall into central Angola (Revermann et al. 2016). It is likely that the *Terminalio sericeae-Schinziophyetum rautanenii* forms part of the Zambezian *Baikiaea* woodlands ecoregion because of the presence of *Pterocarpus angolensis* and *Schinziphyton rautanenii*, whilst the three other associations form part of the Kalahari *Acacia-Baikiaea* woodlands ecoregion.

The vegetation of the Namibian Thornbush savannah is presently under review, and will include the higher syntaxonomic placement of the four associations described as part of the Thornbush – Karstveld transition. A basis for this revision is the earlier work by M. Strohbach (2002), but will also include further data and more recent publications covering parts of the Namibian Savanna Woodlands ecoregion (Olson et al. 2001; Spriggs 2001c; Strohbach 2014, 2019, 2021).

The higher syntaxonomic placement of the grass- and wetland types stays problematic. The *Sporobolus* dominated (*ishana* type) grasslands have been best studied to date, with accounts available from the Etosha Pan halophytic ecoregion, the Cuvelai Basin, the Naye-Naye panveld and also from the Zambezi Region in north-eastern Namibia (Le Roux et al. 1988; Schlettwein 1991; Hines 1992; Clarke 1999; Strohbach 2000; Olson et al. 2001; Spriggs 2001a, Lushetile 2009; Kangombe 2010). Although a general description of wetland types exists for north-eastern Namibia, this does not include detailed floristic descriptions (Hines 1993). Additionally, compounded by limited data, the three wetland communities found within this study could not be formally described.

The two mesic grassland associations described here are clearly part of (possibly remnants of?) the Highveld grasslands ecoregion in Souh Africa (Bowie and Frank 2001; Olson et al. 2001; Mucina and Rutherford 2006). Yet, through the occurrence of specific species either endemic to the Otavi Mountains or not known to occur in the Highveld grasslands, these two associations are confidently described as new associations. As a comprehensive higher syntaxonomic classification of the entire grassland ecoregion of South Africa seems lacking (Mucina and Rutherford 2006), no placement in such a system could be attempted.

The general lack of syntaxonomical descriptions in neighbouring Botswana and Angola, together with a lack of a comprehensive syntaxonomic overview of especially the grassland and bushveld ecoregions in South Africa, makes a comparision of the present Namibian syntaxonomic classification to similar southern African vegetation difficult.

With 889 observed species within roughly 25,000 km^2, the Karstveld is extremely species rich within the arid- to semi-arid Namibian context (Mendelsohn et al. 2002; Craven and Vorster 2006). It is comparable in richness to the Khomas Hochland in Namibia, where 914 species have been observed over roughly 31,000 km^2. The Khomas Hochland, however covers a far bigger variety of habitat types along a steep rainfall gradient (Strohbach 2021). As this survey was only on a reconnaissance scale, the actual number of species occurring here could be vastly higher. Yet only fractions of these ecosystems are formally protected within the Etosha National Park, putting a high importance on private nature reserves and conservancies within this area. Three such freehold conservancies exist, being the Otavi Mountain, Ngarangombe and Omirunga conservancies (Shaw and Marker 2010; NACSO 2022). The Karstveld plains, including the Omuramba Ovambo ecosystem, is however virtually unprotected (Shaw and Marker 2010).

Data availability

The data used for this publication forms part of the Namibian Phytosociological Database (GVID ID AF-NA-001) and can be provided on request by the corresponding author. The full relevé data is also reproduced in Appendix 1 as phytosociological table. All data of GVID ID AF-NA-001 has been shared with the sPlot database as well as the GBIF database.

Author contributions

B.S. planned the research, B.S. and M.S. conducted the field sampling, M.S. did the initial data analysis and description for the Thornbush savanna, whilst B.S. reanalysed the entire data set and drafted the manuscript. Both authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
Climate diagrams for several localities within the Karstveld of Namibia
Link: https://doi.org/10.3897/VCS.99045.suppl1

Supplementary material 2
Phytosociological tables of the five major groupings
Link: https://doi.org/10.3897/VCS.99045.suppl2

Supplementary material 3
Full synoptic tables of the five major groupings
Link: https://doi.org/10.3897/VCS.99045.suppl3