

The mountain top flora and vegetation of the remote Ovahimba Highlands in the Kaokoveld Centre of Endemism: a reconnaissance

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Abstract

The Kaokoveld Centre of Endemism is a hotspot of biodiversity and endemism, largely underexplored while new species are continually described. A reconnaissance survey of flora and vegetation was undertaken on three remote mountain tops of the western Great Escarpment: Cafema and Tchamalindi in Angola's Iona National Park, and Middelberg in the Otjihipa Range of Namibia, providing the first floristic account for Serra Cafema. Vegetation cover and woody vegetation structure were assessed, and botanic surveys were performed. Previously collected occurrence data allowed to determine Kaokoveld endemics.

Commiphora woodlands were found on the mountains despite the semi-desert on the surrounding plains. Woodlands were interspersed with montane savanna and on Cafema with sclerophyll dwarf shrubs. Our study provides the first assessments of species richness in the Ovahimba Highlands with the highest for Serra Cafema: 56 species per 1000 m² compared to 47 species per 1000 m² for the other mountains. Species composition, especially Cafema, is very different from the surrounding lowlands, making a case for a satellite population of Afromontane vegetation. The distribution of sixteen species was expanded from Namibia to Angola. Of the 285 taxa, 12% were Kaokoveld endemics, of which 65% woody species, both relatively high compared to Afromontane vegetation in Eastern Africa. Only a fraction of the flora could be recorded and more surveys after good rainfall are required, especially considering the threats of climate change and overgrazing. The mountain flora deserves priority conservation efforts to protect endemic plants and old taxa that survived in these refuge sites.

Keywords: Afromontane; Escarpment; endemic; floristic diversity; Iona National Park

1. INTRODUCTION

The cross-border Kaokoveld Centre of Endemism is one of the world's hotspots of biodiversity and species endemism (Maggs *et al.*, 1998; Craven, 2002; UNEP-WCMC, 2013). The exact extent of this centre of endemism is uncertain, but in its broadest definition, the Kaokoveld stretches over about 1000 km from the Kuiseb River in central Namibia to Benguela in Angola and from the Atlantic Ocean to the western Great Escarpment in the east (Craven, 2009). The high biodiversity of the Kaokoveld can be explained by a rapid transition from the arid coast that is seasonally influenced by fog to a semi-arid and mountainous escarpment with mountain tops rising to 2500 m.a.s.l.

Because of the size, remoteness and inaccessibility of the Kaokoveld, it is largely underexplored and new species continue to be found. Two decades ago, Craven (2002) established a list of more than 1000 vascular plants for the Namibian Kaokoveld of which 24 were considered to be endemic to the area. Since then, at least 33 additional endemic plant species have been described for the Kaokoveld, many of them in mountainous areas (Swanepoel, 2005, 2006a, 2006b, 2007a, 2007b, 2008a, 2008b, 2009a, 2009b, 2013, 2015, 2019, 2020; Van Jaarsveld and Swanepoel, 2007, 2012; Swanepoel and Kolberg, 2011; Tripp and Dexter, 2012; Swanepoel *et al.*, 2015, 2019, 2021a; Swanepoel, W., De Cauwer, V. & Van Wyk, A.E. 2021a. A new species of *Osteospermum* subgen. *Tripteris* (Asteraceae: Calenduleae) from the Namib Desert, Namibia. *Phytotaxa* **487** (3): 185–194. [Crossref], [Web of Science ®], [Google Scholar], 2021b, 2022; Kolberg and van Slageren, 2016; Darbyshire *et al.*, 2019, 2021; Swanepoel and De Cauwer, 2019; Swanepoel and Van Jaarsveld, 2019, 2020; Tripp and Darbyshire, 2020; Swanepoel and Manzitto-Tripp, 2022). Few quantitative vegetation surveys have been performed in the Namibian Kaokoveld with widely spread sample plots that are mainly located in the lowlands (Burke, 2005; Becker and Müller, 2007; Jürgens *et al.*, 2018; Hamutenya, 2021). One study focusing on mountain vegetation in northwestern Namibia (Burke, 2005) stressed the importance of investigating more and particularly higher mountains to obtain a better mountain vegetation description.

Information on the biodiversity and endemism in the Angolan part of the Kaokoveld is even more incomplete than the Namibian component (Clark *et al.*, 2011). Hardly any field research was done during the war years, which started with Angola's independence in 1975 and continued until 2002. After that, biodiversity research in Angola resumed but the coverage of remote regions, such as Iona National Park, remained poor (Huntley *et al.*, 2019). The main vegetation surveys of the last decades in Iona National Park were in the Tchamalindi mountains in 2009 (Van Jaarsveld, 2010; Huntley *et al.*, 2019), at the biodiversity observatories of Espinheira and Tundavala since 2014 (Jürgens *et al.*, 2018) and during the SCIONA project (De Cauwer and Lages, 2018; António, 2022).

The mountains of the Kaokoveld form part of the Great Escarpment of southern Africa, known to host many of the region's endemic plants (Clark *et al.*, 2011). Ongoing studies estimate that there are around 200 plant species endemic to the Angolan escarpment area of the Kaokoveld (Goyder and Gonçalves, 2019). Many of Namibia's endemic plant species are associated with mountains, especially if these mountains are located in deserts. The highest mountain in Namibia, the Brandberg, is part of the Kaokoveld Centre of Endemism and is situated in a semi-desert. It has the highest known concentration of endemic species (74) in Namibia (Craven and Vorster, 2006).

Conservation in biodiversity hotspots has become of global importance considering the world's increasing species extinction and defaunation (Dirzo *et al.*, 2014; McCauley *et al.*, 2015; Young *et al.*, 2016). Part of the Kaokoveld is to some extent protected by the Skeleton Coast National Park in Namibia and Iona National Park in Angola, which form a Transfrontier Park since 2018. Most of the Namibian part is situated in communal conservancies, such as Marienfluss and Puros. However, despite protection, remoteness and low population density, the vegetation of the Kaokoveld still faces severe threats. Overgrazing by livestock of the local population, especially in the plains, has caused a decrease in herbaceous cover and palatable woody species while it has led to the decline of many perennial grass species (Malan and Owen-Smith, 1974). Consequently, the reliance of herders on the river and mountain vegetation has increased (Malan and Owen-Smith, 1974), especially during the prolonged drought conditions that occurred in the Kaokoveld since 2011 (Thompson, 2021). Climate change will place additional pressure on range-restricted species, especially those situated in areas with steep rainfall gradients, such as the Escarpment (Turpie *et al.*, 2010). Furthermore, illegal succulent harvesting is on the rise and, while already a major problem in South Africa, is becoming a problem in Namibia as well. Hence, assessments of the current status of biodiversity and endemism in the Kaokoveld and its fragile mountain ecosystems are urgently needed.

As a result of an exceptional opportunity, a cross-boundary biodiversity survey was arranged in April 2021 and three of the highest and remotest mountain tops of the Ovahimba Highlands, a mountain range that stretches from southern Angola to northern Namibia (Owen-Smith, 2010), were visited by helicopter. This study gives a quantitative description of the vegetation structure and composition and provides an assessment of the species richness and endemism at the three mountaintops that were visited during our reconnaissance survey.

2. METHODS

2.1. Study area

The Kaokoveld Centre of Endemism is bordered in the west by the Atlantic Ocean and stretches 100 to 150 km due east through the Namib Desert, the pro-Namib and the Great Escarpment to the inland plateau of southern Africa, while from south to north it stretches from the Kuiseb River to Benguela (Craven, 2009). Elevation ranges from sea level to 2050 m.a.s.l. at Serra Cafema, 2065 m.a.s.l. in the Baynes mountains of the Ovahimba Highlands, 2573 m.a.s.l. in the southern Kaokoveld on Brandberg Mountain and 2600 m.a.s.l. at Morro Moco in the northern Kaokoveld. It is a hyper-arid to arid area with mean annual rainfall ranging from 30 mm at the Skeleton Coast to 300 mm in the east (Wassenaar *et al.*, 2021). Rain falls during summer but is highly erratic and patchy, while the western areas regularly receive fog from the cold Benguela Current. The landscape varies from desert in the west, shrubland and sparse grasslands in the Pro-Namib to arid savanna on the highlands and inland plateau in the east.

The mountain ranges of our study were chosen because they are underexplored, while they reach among the highest elevations in the Kaokoveld: Middelberg of the Otjihipa Range in Namibia, and the Tchamalindi and Cafema mountain ranges, or Serra in Portuguese, in Angola (Figure 1). The study areas all form part of the Ovahimba Highlands and are surrounded by vast stretches of drylands. They were defined altitudinally by the 1100 m contour line, a similar height used to delineate the eastern side of the Nyanga massif (Clark *et*

al., 2017). The contour was derived in a GIS from the 30 m resolution Shuttle Radar Topographic Mission (SRTM) data. Access to the peaks of the study areas is notoriously difficult as there are no roads with the terrain extremely rocky, and the heat and drought perilous for human explorers. There are few large mammals in the mountains, with exception of chacma baboons, Hartmann's mountain zebra and greater kudu.

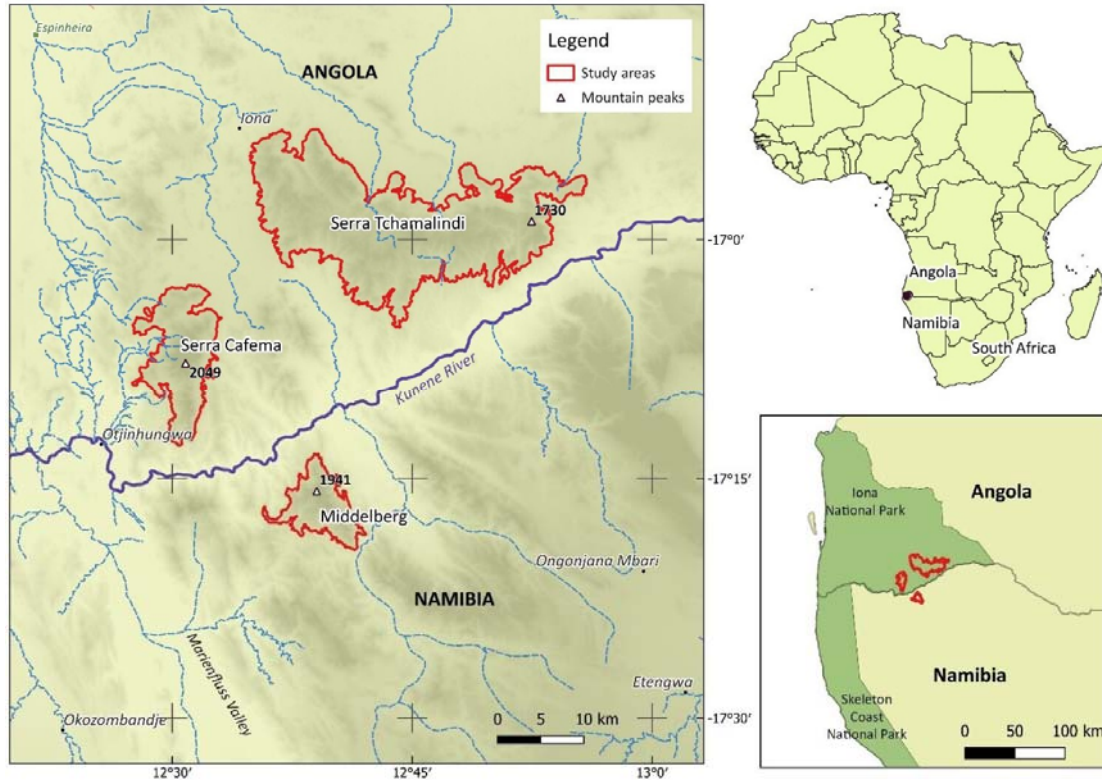


Figure 1. Overview of the study area: the three visited mountain tops of the Ovahimba Highlands in the northern Kaokoveld at the border between Namibia and Angola. The study areas are delineated by the 1100 m contour line.

The Otjihipa mountain range in Namibia is bordered by the Kunene River in the north and the Marienfluss valley in the west (Figure 1). The team visited one of the highest areas of the easternmost part of this range, a roughly 12 km long, northwest-southeast ridge with the highest point a peak in the northwest at circa 1941 m.a.s.l. Geological formations of quartzite and dolomite meet on top of this ridge, creating different soil types. The ridge was named Middelberg by two of the co-authors and covers approximately 52 km².

Tchamalindi is a 40 km long, crescent-shaped west–east quartzitic sandstone range located north of the Kunene River in Iona National Park in Angola, covering approximately 406 km² (Figure 1). The undulating upper plateau has an elevation of 1700 to 1900 m.a.s.l. and is surrounded by sheer cliffs. Various drainage lines cut through the cliffs from the central west–east watershed forming deep gorges in places. The team visited the easternmost section of this range and set up camp at about 1420 m.a.s.l., as the helicopter could not land higher up the mountain where it was covered with a continuous tree layer. Due to the sheer size of Serra Tchamalindi and time constraints, a relatively very small area of the mountain was investigated.

Cafema is a 2050 m.a.s.l. high granite mountain situated on the western edge of the escarpment zone in Iona National Park in Angola, opposite the Marienfluss Valley in Namibia, covering approximately 100 km². At 85 km from the coast, it was the closest of the three mountain tops to the Atlantic Ocean. The 7 km north–south plateau gradually slopes from 2050 m.a.s.l. in the south down to 1300 m.a.s.l. in the north and receives fog and cool west wind from the Atlantic Ocean. Camp was set up within 100 m of the highest point.

2.2. Vegetation survey and data analysis

A vegetation survey was done in April 2021 in three plots on each of the three mountain tops to describe the species richness and woody vegetation structure. The number of plots was constrained by the complex and expensive nature of the expedition by helicopter, resulting in a limited team size and field work duration. The vegetation survey was done by one person. The plots were positioned within walking distance from each camp and their location was chosen after one day exploration walks with the botanical team, which included experts with considerable field experience in the area. The plots were placed to represent the variability in the vegetation near the camp, sometimes representing different plant communities. The plot design of the Namibian forest inventory method (Burke *et al.*, 2001) was followed because the boundaries are easy to establish by one person in the field, especially with a laser range finder. Sample plots were circular with a radius of 20 m (i.e. 1257 m²). The position of the central point was recorded by GPS.

All vascular plant species in the nine plots, herbaceous and woody, were recorded and their abundance was estimated as projected cover (%), without the use of a scale (Strohbach and Kangombe, 2012; Revermann *et al.*, 2017; Jürgens *et al.*, 2018). Species that only occurred beyond the 17.84 m radius of the sample plot were recorded to allow determining species richness for the commonly used plot size of 1000 m² (Jürgens *et al.*, 2013; Strohbach, 2021) facilitating comparisons with other areas. The species were grouped according to life form using four main categories: tree, shrub, herb, and grass. The species richness was determined as the number of species for the inner 1000 m² sample area.

Additionally, a survey of the woody vegetation was performed using a forest inventory methodology that allows to characterise the woody vegetation composition and structure and monitor changes over time (Burke *et al.*, 2001; SEOSAW partnership, 2021). Measurements were taken of all tree stems for the three plots at Middelberg and two plots at Tchamalindi and Cafema respectively. Woody plants were considered a tree when the diameter at breast height (DBH), which is 1.3 m above the ground, was larger than 5 cm as per the Namibian Forest Inventory protocol (Burke *et al.*, 2001). All tree stems, also from multi-stemmed trees, were measured by recording the stem circumference at breast height with a tape measure and the tree height with a laser range finder. Observations of tree damage, cause of tree damage and phenology were recorded for each stem. Tree density was determined by converting the number of stems in the plot to the number of stems per hectare. Basal area was calculated as the sum of the cross-sectional areas of all tree stems at breast height within the plot and converted to an area per hectare (m².ha⁻¹). Basal area is a useful variable to describe vegetation structure as it is correlated to tree density and biomass (Köhl *et al.*, 2006).

2.3. Botanical survey

Simultaneously with the vegetation survey, the botanical team did a qualitative exploration of the flora within a day's walking distance from each base camp for two to three days to

establish a comprehensive plant list for each mountaintop. Observed plant taxa were recorded and identified up to the infraspecific level where possible. Samples were collected for identification and storage in the Herbarium of Lubango (LUBA) and the National Herbarium of Namibia (WIND). Species identification was assisted by consultation of online databases and input from experts of specific taxa. Taxonomy followed the World Flora Online (WFO, 2022).

2.4. Phytogeography and determination of floristic endemism

In this study, species were considered endemic if they only occur in the Kaokoveld and nowhere else. Plant endemism on individual mountains in tropical Africa is exceptional (White, 1978) and hence, endemism was not evaluated per mountain. The distribution of each species was determined with own species occurrence data collected during this and previous surveys in Angola and Namibia (De Cauwer and Becker, 2018; De Cauwer and Lages, 2018; De Cauwer, 2020; Fillipus, 2021; Wassenaar *et al.*, 2021; António, 2022), the publication Plants of Angola (Figueiredo and Smith, 2008), and online databases, especially the Namibian Tree Atlas project (Curtis and Mannheimer, 2005), GIBF (<https://www.gbif.org/>), iNaturalist (<https://www.iNaturalist.org/>) and the African Plant Database (<https://africanplantdatabase.ch/>). The species' ranges allowed identifying the plants endemic to the Kaokoveld. The most range-restricted and endemic species found at the three mountain locations were highlighted and their IUCN conservation status was determined based on the red list categories and criteria (IUCN, 2012).

3. RESULTS

3.1. Vegetation and plant taxa on Middelberg, Otjihipa range

The vegetation observed at Middelberg consists mainly of open *Commiphora* woodland with a canopy height of about 4.5 m. Plots M1 and M2 were located on dolomite with western exposure and plot M3 was on sandstone with eastern exposure. The most common trees in the sample plots were *Euphorbia guerichiana* (paper bark euphorbia) and *Commiphora* species, especially *C. africana* and *C. mollis* (Table 1). The mean tree stem density for all plots was 196 stems.ha⁻¹ and the mean basal area was 1.6 m².ha⁻¹. Although not part of the ten most prominent species, the tallest tree was a *Maerua* sp., most probably *M. schinzii*, with a height of 5.2 m, growing through the canopy of a *Vachellia recifensis*. The trees with the largest stem diameter were *Euphorbia eduardoi* (Kaoko tree euphorbia) with a DBH of 23 cm and *Commiphora glaucescens* (blue-leaved corkwood) (Table 1). Most *E. guerichiana* trees were damaged at the roots and lower stem, probably by porcupines, while small pieces had been cut away from branches of several *C. mollis* (velvet corkwood) trees, probably by herders to quench their thirst. All trees were still in leaf, although most had lost their fruit with exception of a few individual *Commiphora* sp.

Table 1. Woody vegetation structure in the sample plots on Middelberg (M1, M2, M3), Tchamalindi (T1, T2) and Cafema (S1, S3) with number of trees, mean stem diameter at breast height (DBH) and maximum height for the ten most prominent tree species. Standard deviation is indicated between brackets.

Species	Number of trees in a plot							Mean DBH (cm)			Maximum height (m)		
	M1	M2	M3	T1	T2	S1	S3	Middelberg	Tchamalindi	Cafema	Middelberg	Tchamalindi	Cafema
<i>Colophospermum mopane</i>					26				10.6 (3.8)			5.4 (0.6)	
<i>Commiphora africana</i>		2	6	5	2	7	1	8.4 (1.5)	10.6 (3.4)	10.5 (1.7)	2.8 (0.3)	3.7 (0.6)	3.5 (0.4)
<i>Commiphora glandulosa</i>	3	2		4	22			10.1 (3.0)	8.4 (2.1)		3.3 (0.3)	4.3 (0.6)	
<i>Commiphora glaucescens</i>	2	1				3	1	15.8 (6.9)		11.6 (4.4)	4.8 (0.8)		2.3 (0.1)
<i>Commiphora mollis</i>	3	3	2	6	4	9		10.8 (6.5)	18.5 (13.9)	13.1 (1.7)	4.5 (0.9)	5.8 (1.0)	4.0 (0.6)
<i>Commiphora ob lanceolata</i>		3	4					5.4 (0.5)			3.0 (0.4)		
<i>Cyphostemma currorii</i>	2	4				4	2	12.5 (4.1)		18.2 (5.1)	2.5 (0.4)		3.7 (0.6)
<i>Euphorbia guerichiana</i>	9	4	6			5	9	6.5 (1.3)		8.3 (2.6)	3.9 (0.4)		4.5 (0.6)
<i>Ozoroa crassinervia</i>						2	4			12.9 (8.4)			4.8 (1.1)
<i>Terminalia prunioides</i>					15				8.4 (2.1)			5.6 (0.7)	
For all species	23	24	27	28	74	39	21	9.7 (4.7)	10.5 (5.9)	11.1 (4.9)	5.2 (0.7)	5.8 (1.0)	5.9 (0.8)

Table 2. Plant species with the highest mean cover (%) for three sample plots on Middelberg, three at Tchamalindi and three at Cafema, with the mean for all plots.

	Cover (%)			Mean
	Middelberg	Tchamalindi	Cafema	
<i>Melinis longiseta</i> subsp. <i>bellespicata</i>	0.3	11.3	0.2	3.9
<i>Commiphora mollis</i>	1.3	5.3	3.3	3.3
<i>Colophospermum mopane</i>	0.0	6.7	0.0	2.2
<i>Euphorbia guerichiana</i>	3.5	0.3	2.8	2.2
<i>Pappea capensis</i>	0.0	0.0	6.7	2.2
<i>Commiphora glandulosa</i>	0.8	5.8	0.0	2.2
<i>Commiphora africana</i>	0.7	2.2	3.3	2.1
<i>Combretum apiculatum</i>	0.8	5.2	0.0	2.0
<i>Ozoroa crassinervia</i>	0.0	0.0	4.7	1.6
<i>Euphorbia mauritanica</i>	0.0	0.0	4.0	1.3
<i>Urochloa brachyura</i>	0.0	3.7	0.0	1.2
<i>Euryops namibensis</i>	0.0	0.0	3.0	1.0
<i>Grewia discolor</i>	0.2	1.4	1.2	0.9
<i>Peltophorum africanum</i>	0.0	0.2	2.3	0.8
<i>Terminalia prunioides</i>	0.0	2.3	0.0	0.8
<i>Commiphora glaucescens</i>	0.8	0.3	1.2	0.8
<i>Pelargonium vanderwaltii</i>	0.0	0.0	2.2	0.7
<i>Erythrina decora</i>	0.3	0.0	1.7	0.7
<i>Setaria</i> sp.	0.0	0.0	2.0	0.7
<i>Cyphostemma curronii</i>	1.0	0.0	0.9	0.6
<i>Distephanus angolensis</i>	0.0	0.0	1.8	0.6
<i>Sclerocarya birrea</i>	1.8	0.0	0.0	0.6
<i>Solanum</i> sp.	0.2	0.1	1.5	0.6
<i>Rhigozum brevispinosum</i>	0.0	1.7	0.0	0.6

The plots on Middelberg had a high plant species richness: 78 different plant species were recorded in the sample plots with an average of 47 species per 1000 m². Species richness was fairly similar for all plots (43–49 species per 1000 m²) with most of the species (53%) herbs. The species with the highest average coverage are shown in Table 2. *Euphorbia guerichiana* and *Sclerocarya birrea* (marula) contributed most to the vegetation cover of the plots at Middelberg.

A total of 147 plant species were recorded during the botanical survey on Middelberg, most of them herbs and representing 57 families (Appendix 1). Most of the recorded species (10.1%) belong to the Fabaceae, while the Asteraceae, Burseraceae, Malvaceae and Poaceae are the next best-presented plant families with each 5.4% of the species. Most plants were identified up to at least genus level, although several species are still regarded as uncertain because of insufficient material. Amongst the most exciting finds were *Cussonia angolensis* (Angolan cabbage tree), *Olea europaea* subsp. *cuspidata* (wild olive) and *Combretum molle* (hairy bush-willow), all new records for the Kaokoveld escarpment zone with the latter a new record for the Kaokoveld. *Cussonia angolensis* was previously only known from the Baynes Mountains in Namibia further to the east although other populations have been observed in Angola (African Plant Database, 2022).

3.2. Vegetation and plant taxa on Serra Tchamalindi

The main vegetation observed near the camp on Tchamalindi was mopane savanna, while *Commiphora* woodland was found at higher elevations. The woodland was interspersed with montane savanna in the rockiest areas. The sample plots were positioned at elevations ranging from 1400 to 1820 m.a.s.l. The woody vegetation inventory was not performed in a plot within montane savanna (T3). The mean canopy height in the other two plots was about 5.5 m, the mean tree stem density for the two plots was 271 stems.ha⁻¹ and basal area 4.6 m².ha⁻¹, triple the value of the basal area of the plots on Middelberg. The basal areas in T1 and T2 were similar, despite the difference in stem density (Table 1). The most common trees in the sample plots were *Colophospermum mopane* (mopane) and *Commiphora glandulosa* (tall common corkwood). The tallest tree was a *C. mollis*, which was also the tree with the largest stem diameter (DBH = 29 cm). Several trees showed signs of distress, although the reason was not obvious, most probably a combination of drought and insect damage. All trees were still in leaf, although most had lost their fruits with exception of a few individuals of *Commiphora* sp.

More plant species ($n = 96$) were recorded in the sample plots than at Middelberg, with a similar average of 46 species per 1000 m² that varied little between the plots. Thirty-six percent of the species consisted of herbs as Tchamalindi had more woody species (52%) than the plots on Middelberg where 37% of the species were woody. The species with the highest average coverage were the grass *Melinis longiseta* subsp. *bellespicata* and *C. mopane* (Table 2).

A total of 152 plant species were recorded during the botanical survey at Tchamalindi, representing 50 families (Appendix 1). The floristic composition was very similar to that of Iona peak, as observed during the expedition in 2009 (Van Jaarsveld, 2010). Similar to Otjihipa, most of the recorded species (11.1%) belong to the Fabaceae, while the Malvaceae are the next best-presented plant family (7.2%). The Burseraceae, Asteraceae, Poaceae, Euphorbiaceae and Capparaceae are also well represented with 5.9% of the species for the former, and 5.2% for the four latter families. An important find is the first record for Angola

of the succulent tree *Sesamothamnus leistneri* ined., previously thought to be a Namibian endemic. The Kaokoveld endemic shrub *Turnera oculata* var. *paucipilosa* was very common near the base camp at Tchamalindi.

3.3. Vegetation and plant taxa on Serra Cafema

The upper slopes of Cafema have a surprising amount of vegetation, consisting of a mosaic of sclerophyll dwarf shrubs and montane savanna vegetation with large stemmed *Ozoroa crassinervia* (Namib resin tree). Vegetation observed lower down the mountain can be described as arid savanna, although it harbours a variety of ecological niches that can accommodate large trees. The sample plots were positioned lower than the base camp, ranging from elevations of 1920 to 1850 m.a.s.l. and with different exposures. The tree layer had a canopy height of about 4.5 m, a mean tree stem density of 159 stems.ha⁻¹ and a mean basal area of 2.8 m².ha⁻¹. Mean DBH was also slightly higher than at Middelberg (Table 1). The most common trees in the sample plots were *E. guerichiana* and *C. mollis*. The tallest tree as measured in two plots was a *Boscia* species, most probably *B. tomentosa* (hairy shepherd's tree), of 5.9 m high. Identification was difficult because the tree had few leaves very high up. The species with the largest stem diameter was a Namib resin tree with a DBH of 27 cm. All trees were still in leaf, although most had lost their fruit. Several trees showed signs of distress, probably a result of the extended drought in the region.

More plant species ($n = 117$) were recorded in the sample plots on Serra Cafema than at the two other mountains, with an average of 56 species per 1000 m², a value that did not vary much between the three plots. Similar to Middelberg, 49% of the species were herbs. The species with the highest average coverage were *Pappea capensis* (jacket-plum) and *O. crassinervia* (Table 2).

A total of 140 plant species were recorded during the botanical survey at Serra Cafema representing 52 families (Appendix 1). Most of the recorded species belong to the Fabaceae (9.2%) and Asteraceae (9.2%). The next best-presented plant families were the Burseraceae, Poaceae, Euphorbiaceae and Lamiaceae with each 5.7% of the species. The sclerophyll elements are amongst others represented by *Euryops namibensis*, *Eriocephalus* sp., and *Thesium* sp. Another *Turnera* is common here (*Turnera oculata* var. *oculata*). Large individuals of tree species such as *P. capensis* and *Olea europaea* subsp. *cuspidata* (wild olive) were encountered. A new species was found: *Coleus serra-cafemaensis* (Van Jaarsveld *et al.*, submitted). Another noteworthy record is that of *Euphorbia leistneri*, a rare species of which the Serra Cafema population is only the second recorded locality, previously known only from the Kunene River Valley close to Epupa Falls in Namibia (Möller and Becker, 2019). Another surprise was the tall *Euphorbia monteiroi* subsp. *brandbergensis* that was previously only known from the Brandberg and the Erongo mountains further south in Namibia (Bruyns, 2022).

3.4. Floristic endemism

Of the 285 taxa recorded during this study, 34 or 11.9% are endemic to the Kaokoveld, as indicated in Appendix 1. Most of the endemic taxa (65%) are woody taxa. The best-represented families were the Euphorbiaceae (8) and the Burseraceae (4). The endemic taxa with the smallest areas of occupancy are *Commiphora otjihipana*, *Pelargonium vanderwaltii*, *Euphorbia monteiroi* subsp. *brandbergensis*, *Euphorbia leistneri*, *Aloe corallina* and *Aloe omavandae*. All except *A. omavandae* are known from only two to three locations, while all

of them have an extent of occurrence that is much smaller than 5000 km², hence falling under the endangered IUCN red list category. There is also convincing evidence that several species new to science have been found, with one already described (Van Jaarsveld *et al.*, submitted). However, more material, especially flowers and fruit, is needed for further investigation.

4. DISCUSSION

4.1. Vegetation structure and composition

The small number of plots at each mountain top did not allow a quantitative vegetation classification, however, the vegetation survey in combination with the botanical survey allowed to give a good characterisation of the vegetation at the visited mountain locations. The genus *Commiphora* was well-represented in all three study areas with fourteen species and they contributed a large part to the tree cover, even on Serra Cafema. The *Commiphora* woodlands contrast sharply with the semi-desert vegetation in the surrounding lowlands (De Cauwer and Becker, 2018; De Cauwer and Lages, 2018; Wassenaar *et al.*, 2021; António, 2022). The highest basal area, a proxy for biomass, was recorded for two plots at Tchamalindi, the most eastern location visited and with the highest rainfall. The two plots are representative of the woodlands dominating south-eastern Tchamalindi, as observed by helicopter and exploration walks. The largest trees were found at Serra Cafema although they are restricted to the most sheltered valleys and gulleys, where no tree measurements were done.

Most recorded species (9.4%) were from the Fabaceae family, as in the lowlands of Iona National Park (António, 2022). On Cafema, the Asteraceae were more represented than on the other mountain sites. They formed the dominant family together with the Fabaceae, similar to other southern African summer rainfall montane areas (Clark *et al.*, 2017).

Although the signs of human and livestock impact on the vegetation were limited, it was observed that herders do visit the highest tops of the mountains. The common occurrence of species such as *Tribulus terrestris* and *Achryanthes aspera* are signs of regular grazing, although they were not abundant (< 0.01% cover), not even in shaded locations, which would be a sign of overgrazing (Burke 2005; Aerts *et al.*, 2006).

4.2. Species richness and floristic composition

The species richness in the sample plots was 47 species per 1000 m² for Middelberg and Tchamalindi and 56 species per 1000 m² for Cafema. This is much higher than for the desert vegetation in the southern Kaokoveld Centre of Endemism with 0 to 21 species per 1000 m², depending on the vegetation type. It is also higher than found for the Brandberg, with 27 species per 1000 m² (Jürgens *et al.*, 2013). Species richness was similar to that of the vegetation found in the Khomas Highland proper, an eastern extension of the escarpment towards Windhoek (Strohbach, 2021).

The transitions between plant communities observed on the mountain tops are rapid and are probably caused by the steep temperature gradients and the differences between south and north-facing slopes, explaining to a large extent the large numbers of species recorded. While the elevation range of the sample plots was highest at Tchamalindi (240 m), other factors influence species richness such as different geologic formations at Middelberg, and the occurrence of fog at Serra Cafema. The latter is a typical phenomenon for the Succulent

Karoo and is caused by an oceanic influence that buffers extreme temperatures and creates a high relative air humidity during late night and early morning. The Succulent Karoo is characterised by a large number of leaf succulent taxa, including *Pelargonium* species (Jürgens, 1991), which we found at Serra Cafema. Although the Succulent Karoo has been described to include Afromontane regions further away from the coast in southern Namibia (Jürgens, 1991), such a region was not described for northern Namibia or southern Angola. Yet, the climatic conditions found on Serra Cafema do fit those of the Succulent Karoo well, creating habitats perfectly suited to temperate species.

The flora contained taxa typical for different phytogeographical zones, especially the Nama Karoo and Sudano-Zambezian regions, but also the Succulent Karoo on Serra Cafema. Taxa characteristic of the Nama-Karoo were common on all three mountains and include *Vachellia reficiens*, *Moringa ovalifolia*, and *Maerua schinzii* (Jürgens, 1991; Burke, 2005). Yet, the mountain flora is quite distinctive from the surrounding lowlands through the presence of typical highland or tropical species (Swanepoel, 2019; Wassenaar *et al.*, 2021). Typical highland species encountered that are also found at the Brandberg and the Khomas Highland were *Dombeya rotundifolia*, *Ozoroa crassinervia*, and *Olea europaea* subsp. *cuspidata* (Strohbach, 2021; Craven and Craven, n.d.).

According to White (1978), Afromontane vegetation is characterised by the presence of Afromontane species, species endemic to African mountains or species that are absent from the surrounding lowlands. There are at least 4000 Afromontane species on the African continent, however, the total flora is not known while the majority of the species appears to be based on the mountain flora of the eastern Great Escarpment (White, 1978), for which much more floristic data are available. Few of the Afromontane species or genera of Eastern Africa were found during this expedition. Shared genera are for example *Nuxia*, *Maytenus*, *Olea*, *Euryops* and *Justicia*, and a few species, such as *Steganotaenia araliacea*, *Aeollanthus buchnerianus* and *Leonotis ocymifolia* (White, 1978; Aerts *et al.*, 2006; Clark *et al.*, 2017). Well-developed Afromontane vegetation is considered absent in Angola where it is “diluted by the presence of lowland species” (White, 1978, 1981).

4.3. Species’ range expansions

The surveys reported here expand the known range of several species, sometimes also changing their endemic status linked to a country. The known distribution of 16 species was extended from Namibia into Angola for: *Aeollanthus haumannii*, *Commiphora otjhipana*, *Dombeya kirkii*, *Ehretia* cf. *namibiensis*, *Euphorbia caperonioides*, *Euphorbia leistneri*, *Manuleopsis dinteri*, *Ormocarpum kirkii*, *Pavonia columella*, *Pelargonium vanderwaltii*, *Plectranthus dinteri*, *Psiadia punctulata*, the as yet undescribed *Sesamothamnus leistneri* ined., *Stapelia schinzii*, *Sisymbrium capense*, and *Tetradenia kaokoensis*. The range of the subspecies *Euphorbia montei* subsp. *brandbergensis* was also extended into Angola. This confirms that it is more relevant to describe floristic endemism for the transboundary Kaokoveld Centre of Endemics rather than for a country as most of the endemics will occur on both sides of the border.

On the other hand, *Othonna huillensis* was only known from Angola and was found at Middelberg, more than 250 km further south than the most southern known occurrence (iNaturalist 21383874). It was also recently recorded at Mount Namba (LUBA – Goyder, Maiato, Luís, 8631), about 600 km north of the Escarpment, thereby losing its status as Kaokoveld endemic. Another species with a considerable range expansion, whose country

endemic status did however not change, includes *Euryops namibensis*. *E. namibensis* was previously mainly recorded in southern Namibia and South Africa, of which the most northern known occurrence was collected more than 300 km further south in 1983 (BODATSA PRE0651442-0).

4.4. Floristic endemism

At least 11.9% of the taxa recorded were Kaokoveld endemics (Appendix 1). This is a similar ratio to 12.8% found for central Namib (Jürgens *et al.*, 2013), 16% for the Drakensberg Alpine Centre (Carbutt and Edwards, 2004) and 10% for the Manica Highlands (Clark *et al.*, 2017), and much higher than the 1.5% recorded for the Nyanga massif in Zimbabwe (Clark *et al.*, 2017) or 5.3% for Mount Mulanje in Malawi (Strugnell, 2002). The high ratio of woody species (65%), including several trees, is unusual compared to the plant endemics in Eastern Africa (White, 1978; Clark *et al.*, 2017). Furthermore, several species remain to be identified which may increase the number of endemics.

Most occurrences of the endemic species encountered are outliers for their distribution area, similar to the archipelago-like nature of the Afromontane region (White, 1978) and supporting the theory of relic populations (Jürgens, 1997). The large amount of endemic and typical highland species encountered during this study point towards an Afromontane element on the highest elevations of the Ovahimba Highlands, especially Serra Cafema. More floristic surveys and occurrence data are required to demonstrate this. The floristic composition reported here does provide the first indication that the satellite population of Afromontane near-endemics on Serra de Chela, north of Iona National Park (White, 1978) may extend further south.

The present surveys were far from exhaustive to represent the three mountain ranges visited due to the very strict schedule. Moreover, the timing of the survey was not optimal as it took place after nearly ten years of below-average rainfall, including the year of the survey. Long-term botanical studies on the Brandberg have shown that many endemic species are only recorded during exceptional rainy seasons (Burke, 2005). Hence it can be safely stated that only a fraction of the flora was recorded at the sites visited and that especially the list of endemic herbs and small shrubs will be incomplete. Additional surveys, preferably after a good rainfall and in other parts of the study areas, should be performed to get a better understanding of the floristic diversity in the Ovahimba Highlands. April proved to be a good period for plant surveys, although more flowers may be present in March.

In addition, plant material already collected in the herbaria of Namibia and especially Angola need further study (Goyder and Gonçalves, 2019). Such initiatives have become urgent because, while the knowledge of the Kaokoveld plant biodiversity and endemics continues to increase, increased temperatures and aridity (Huang *et al.*, 2017; IPCC, 2021) may already have impacted the fragile Ovahimba mountain ecosystem. With increasing temperatures, many species track their suitable habitats toward higher elevations. This presents a challenge for the more temperate species already at high elevations because they do not have new habitats to colonise, leading to possible species extinction (Manish *et al.*, 2016). Additionally, isolated mountains surrounded by an arid environment serve as refuge areas, areas of reduced impact from man and livestock, where relic populations of many plant and animal species survive (Jürgens, 1997; Burke *et al.*, 1998). However, the increasing reliance of livestock on mountain vegetation may negatively affect these relic populations.

5. CONCLUSIONS

This study gives new insights into the floristic composition and broad vegetation structure of three mountain tops in the Ovahimba Highlands. It provides a reliable list of 285 plant taxa, including one new species, and a first floristic account for Serra Cafema. *Commiphora* woodlands of about 4 to 5 m high were encountered which had higher stem densities and basal areas than the surrounding lowlands. The vegetation composition showed a floristic intermingling of Afromontane elements with subtropical and savanna flora. Although the floristic survey is far from exhaustive, it does demonstrate the high species richness and especially endemism. Species richness was highest at Cafema (56 species per 1000 m²), which has a climate and some plant species typical for the Succulent Karoo. At least six of the 34 endemic taxa fall in the endangered IUCN red list category. Human impact in the area is relatively low compared to other Afromontane regions of the Great Escarpment, however, livestock grazing is increasing as fodder in the surrounding lowlands becomes less reliable because of overgrazing and increasing drought. Better knowledge of the floristic diversity and endemism within the Kaokoveld Centre of Endemism can support global biodiversity conservation efforts, as well as the management of the new Transfrontier Park.

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No potential conflict of interest was reported by the author(s).

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