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Vegetation structure and composition at different elevational intervals in the arid Tankwa Karoo National Park, South Africa

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Abstract

Study area: The study was conducted in the Tankwa Karoo National Park, one of the driest areas in South Africa. Historic overgrazing has resulted in the poor and often degraded state of vegetation in large parts of the Tanqua Karoo region. **Aim:** This study assessed the spatial variation of vegetation structure and composition in the three main vegetation types namely: Tanqua Karoo (TK), Tanqua Wash Riviere (TWR) and Tanqua Escarpment Shrubland (TES), along an elevational gradient. **Method:** Using the point intercept survey method, vegetation cover, plant height, species diversity, life forms, proportions of perennials and annuals were examined in 43 sites, widely distributed in these vegetation types. **Results:** There were 150 vascular plant species belonging to 83 genera and 29 families recorded across all sites. The most diverse vegetation type was TES with 96 species belonging to 61 genera and 26 families. The vegetation structure was comprised mainly of shrubs and dwarf shrubs with a high proportion of leaf and stem succulent species. The mean perennial vegetation cover throughout the study area was 28 and annuals covered 22%, but this cover varied significantly between the vegetation types. The most dominant life forms were chamaephytes, which comprised 64% of all species, with cryptophytes (18%), therophytes (16%) and nanophanerophytes (2%) less abundant. Surveyed sites in the TES showed a clear association with each other but there was an overlap in the species composition and environmental conditions between some TWR and TK sites. This study highlighted the important role of elevation and topography as drivers of vegetation characteristics. **Conclusion:** The findings from this study can be used as a vegetation baseline to identify and prioritise degraded areas for active restoration in order to limit further degradation. Considering climate change, elevational studies may provide additional insight into species dynamics across landscapes.

Taxonomic reference: Plants of Southern Africa Checklist (South African National Biodiversity Institute 2016).

Abbreviations: ANOVA = analysis of variance; GPS = Global Positioning System; LFA = Landscape Function Assessment; NDVI = Normalized difference vegetation index; PCA = principal component analysis; PCo-A = principal co-ordinate analysis; TES = Tanqua Escarpment Shrubland; TK = Tanqua Karoo; TKNP = Tankwa Karoo National Park; TWR = Tanqua Wash Riviere.

Keywords

arid environment, land degradation, life form, spatial variation, Succulent Karoo, vegetation composition, vegetation types

Introduction

The Succulent Karoo Biome is a semi-desert region that extends along the western parts of South Africa and Namibia. It covers an area of approximately 111,000 km^2 on the arid and semi-arid fringes of South Africa's Cape Floristic Region (Mucina and Rutherford 2006) and includes the Tanqua Karoo area, one of the driest landscapes of this biome. The Succulent Karoo Biome recorded the highest diversity value for any arid region in the world (Cowling et al. 1989). It is recognised as one of only two biodiversity hotspots within arid and semi-arid areas (Mittermeier et al. 2004) and comprises about 30% of the world's succulent species (Smith et al. 1993) and has long been identified as a major conservation priority (Cowling and Hilton-Taylor 1994).

It is well documented that arid and semi-arid lands of the world have been subjected to vast and often radical vegetation changes (Li 2018). Overgrazing is considered one of the greatest threats to the indigenous vegetation in the Succulent Karoo (Hoffman and Ashwell 2001; Desmet 2007). As a consequence, vegetation degradation and the declining ability of arid and semi-arid rangelands to support livestock nutritional demands have been major concerns for land managers in southern Africa (Milton and Dean 1995; Hoffman et al. 2009).

The common features of degradation in the Succulent Karoo region are a decline in vegetation cover, and changes in plant species and life form composition (Anderson and Hoffman 2007). This leads to the replacement of palatable perennial grasses and non-succulent shrubs by less palatable or unpalatable, shorter-lived dwarf shrubs and annual species, and as a consequence, an increase in denuded areas and loss of fertile topsoil (Beukes and Ellis 2003; Van Rooyen et al. 2015). Although the vegetation degradation in the area has mainly been ascribed to over-utilisation by livestock and variations in rainfall regime (Kraaij and Milton 2006), the contribution of other environmental factors such as soils, microclimate, elevation and topography exacerbating degradation has received little attention.

Vegetation indicators such as vegetation cover, structure, and diversity are usually considered important indicators of rangeland health and degradation (Schulz et al. 2009). A detailed understanding of vegetation characteristics and their drivers may clarify the current state of an ecosystem and can explain future environmental responses and vegetation dynamics. All of this could benefit conservation management and restoration initiatives in this ecologically significant arid system. Effective restoration programmes in arid areas and sustainable use of its resources cannot be achieved without a thorough understanding of the ecosystem dynamics and the main factors that influence its components and spatial distribution (Saaed et al. 2018).

In the Succulent Karoo context, there is still insufficient information about the vegetation, particularly on in the Tankwa Karoo National Park (TKNP) and adjacent areas. A previous study conducted by Rubin (1998) in the TKNP before the park expanded its boundaries, assessed the physical conditions and major plant communities inside the park, but did not specifically investigate the role of elevation and survey sites were randomly selected in subjectively demarcated plant communities. Other studies in the Tanqua region did not specifically assess the role of elevation either and mainly studied the vegetation in relation to the physical environment such as geology, soils and land types (e.g., Milton et al. 1997; Land Type Survey staff 2010, 2012) with some studies focusing on the impacts of grazing that usually result in the dominance of short-lived plants where disturbance is the highest (Beukes and Ellis 2003; Rutherford and Powrie 2010). Roux and Vorster (1983) and Van der Merwe et al. (2008) studied broad scale vegetation change in the Karoo whereas Kraaij and Milton (2006) assessed these changes on a fine scale in relation to land use change, rainfall and herbivory. The few particularly detailed studies in the TKNP within its recent boundaries were on the floral composition (Bester et al. 2012; Steyn et al. 2013), soil seedbank (Saaed et al. 2018), rangeland resilience and impact of overgrazing (Saeed et al. 2020) and landscape units (Van der Merwe et al. 2015). However, these studies cover small sections of the park and the findings might not be applicable to its overall extent.

Saaed et al. (2018) investigated the composition of the soil seedbank and its role in ecosystem dynamics and restoration potential, while Osman et al. (2019) focused on soil and vegetation differences across a few ecological boundaries in the park. Using NDVI, Saaed et al. (2020) showed that vegetation conditions remained stable in the last 20 years for about 81% of the land despite it being under conservation. The study argued that vegetation productivity is largely a factor of rainfall and not a change in land use from livestock farming to conservation. Saaed et al. (2022a) used Point-Centred Quadrants to show that landscape functionality in the three main vegetation types remained stable due to the low vegetation cover and patchiness, and low mean annual precipitation. However, data and our understanding on vegetation structure and floristic composition and its variation across elevations are still insufficient and scarce across large areas of the park.

The main aim of this study was to assess the vegetation structure and composition in the TKNP in relation to different elevations and determine the variation in these vegetation characteristics within and among the three main vegetation types i.e. Tanqua Karoo (TK, SKv5), Tanqua Wash Riviere (TWR, AZi7) and Tanqua Escarpment Shrubland (TES, SKv4) as described by Mucina and Rutherford (2006). These three vegetation types comprised 94% of the total area of the park and are located at different elevations ranging from the lowland plains to the steep slopes of the escarpment (Saaed et al. 2020).

Methods

Study area

The TKNP in South Africa stretches from the western low-lying plains towards the east to include parts of the Roggeveld escarpment and Roggeveld plateau (Van der Merwe et al. 2008) (Figure 1). In 1986, the TKNP was declared a national park on 27,064 ha of the plains (Rubin 1998), and since then has been extended towards the Roggeveld Mountains reaching 143,600 ha in 2012 (Strauss et al. 2014). According to recent park management consultation, the park has expanded to 163,125 ha in 2022.

From west to east, the physiography of the study area varies greatly from open flats to gently undulating plains, then rises steeply to the escarpment formed by the Roggeveld Mountains (Van der Merwe et al. 2015). The elevation above sea level across the park ranges from 316 m in the open plains to 1,640 m in Roggeveld Mountains. Most of the park lies within the range of 450–750 m above sea level (Strauss et al. 2014).

According to Schulze (1997), the study area is classified as arid, which is characterised by extreme summer aridity, and sporadic and unreliable rainfall, in terms of occurrence and distribution. Rainfall occurs primarily during the winter months, with 67% of the mean annual precipitation falling between March and August. From the meteorological records from 2006 to 2014 (South African Weather Service unpublished data), mean annual rainfall on the Roggeveld plateau ranged between 155–270 mm, and on the low plains ranged between 95–155 mm. The mean July minimum temperature is 6.8°C on the plains and -2.4°C on the Roggeveld Mountains, and the mean January maximum temperature is 36.6°C on the plains and 29°C on the Roggeveld Mountains.

The soils of the area are characterised by young, shallow skeletal features mainly as a result of sheet erosion (Beukes and Ellis 2003). The soils of the plains are shallow lithosols that often include a desert pavement and deep unconsolidated deposits in the alluvial parts. In the eastern high escarpment, the main features are shallow stony lithosols and duplex soils (Francis et al. 2007). The rocky cover of the soil surface becomes more dominant in the escarpment where, at some sites, rock cover exceeds 60% due to the effect of water erosion on the steeper slopes (Saaed 2018).

The vegetation of the region is part of the Succulent Karoo biome. Renosterveld is the only vegetation type in the area belonging to the Fynbos biome, occurring on the uplands of the Roggeveld Mountains (Mucina and Rutherford 2006). The flora of the Succulent Karoo biome comprises mainly shrubs (0.5–1.5 m) and dwarf shrubs (< 0.5 m), generally members of the *Aizoaceae* family, i.e., leaf or stem succulents (Palmer and Ainslie 2006; Van der Merwe and Van Rooyen 2011a), and some are deciduous. Annuals and cryptophytes are common after good rains, while perennial grasses are scarce (Beukes and Ellis 2003). Trees such as *Vachellia karroo* occur along rivers and drainage lines. Within the boundaries of the park, there are six vegetation types: Nieuwoudtville-Roggeveld Dolerite Renosterveld (FRd1), Roggeveld Karoo (SKt3), Roggeveld Shale Renosterveld (FRs3), Tanqua Escarpment Shrubland (SKv4), Tanqua Karoo (SKv5), and Tanqua Wash Riviere (AZi7) (Mucina and Rutherford 2006).

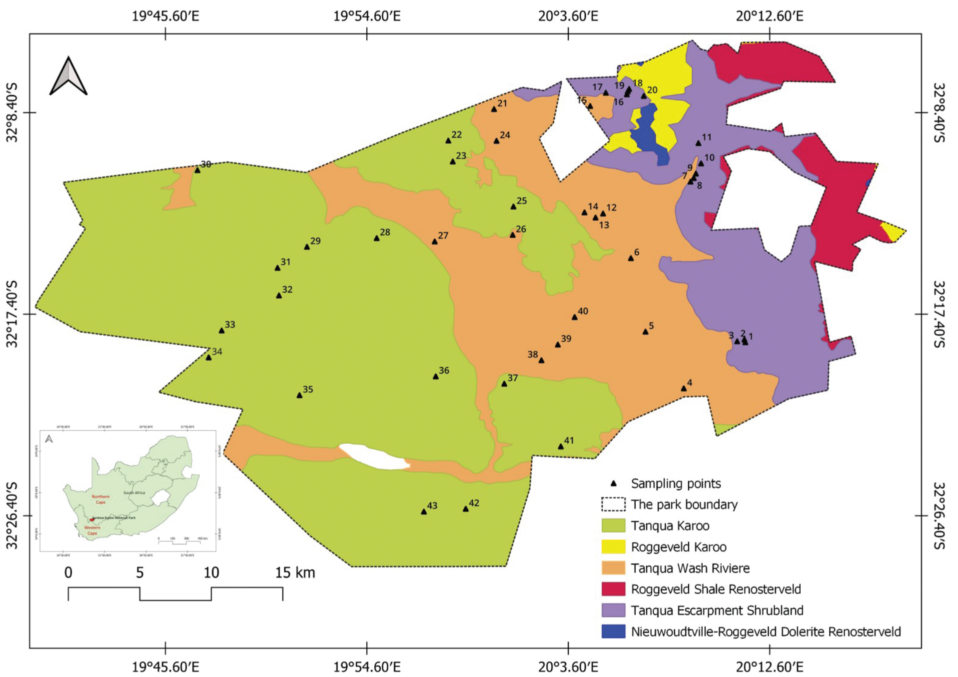

Figure 1. Map of the study area showing the different vegetation types (after Mucina and Rutherford 2006) and the distribution of the sampling sites (black triangle with site number) in the three main vegetation types; the Tanqua Karoo (TK), the Tanqua Wash Riviere (TWR), and the Tanqua Escarpment Shrubland (TES).

Field surveys

The field surveys were conducted at different elevational intervals, covering the three main vegetation types namely: Tanqua Karoo (TK) which occupied the open low-lying plains, Tanqua Wash Riviere (TWR) which occupied the floodplains at the foot of the escarpment and the catchment areas near the rivers and drainage lines, and Tanqua Escarpment Shrubland (TES) which occupied the escarpment of the Roggeveld Mountains. Data were gathered during the spring (September and October) of 2015, the season of commencement of growth for most plant species. The NDVI from Landsat 8 and cadastral boundaries were used to select the areas where the survey sites were to be located. The specific survey points were selected using ArcGIS software that also considered the accessibility to conduct field surveys at the site. The study was conducted at 43 survey sites, widely distributed across the chosen vegetation types. The elevational intervals where the survey sites were located ranged between 338–403 m in TK, 504–717 m in TWR, and 778–1149 m in TES. The TK covered the largest area and comprised 15 survey sites, the TWR and TES comprised 15 and 13 sites, respectively.

A GPS was used to locate the survey sites in the field. Digital photographs of the three main vegetation types (Figure 2) were taken, and environmental attributes such as slope, aspect, and soil surface features were recorded and summarised for each vegetation type. The point intercept survey method was used to conduct the vegetation survey as described by Du Toit (1997). At each of the survey sites, four 100 m line transects (each counting 100 points) started from one point in the landscape and were oriented in four directions with axes aligning with or perpendicular to the main slope of the landscape. The hand-held rod was lowered at the marked points at one-metre intervals on the line. Denuded ground, rock, litter, and canopy-spread cover struck by the rod were recorded. The total observations were 400 strikes at each site.

Vegetation canopy cover was estimated as the percentage of the 400 points surveyed that made contact with a living plant, and the total number of strikes per species was expressed as a percentage of the total number of point observations. To observe variations in the life form composition, each species was assigned to a life form category as defined by Raunkiær (1934) and modified by Mueller-Dombois and Ellenberg (1974), which were nano-phanerophytes, chamaephytes, cryptophytes, and therophytes. Spatial changes in vegetation at different elevational intervals and different vegetation types were investigated in terms of (1) maximum plant height for all species combined, (2) vegetation cover, (3) species richness, (4) Shannon–Wiener index of diversity, (5) species evenness, (6) life form diversity, and (7) presence of succulent species.

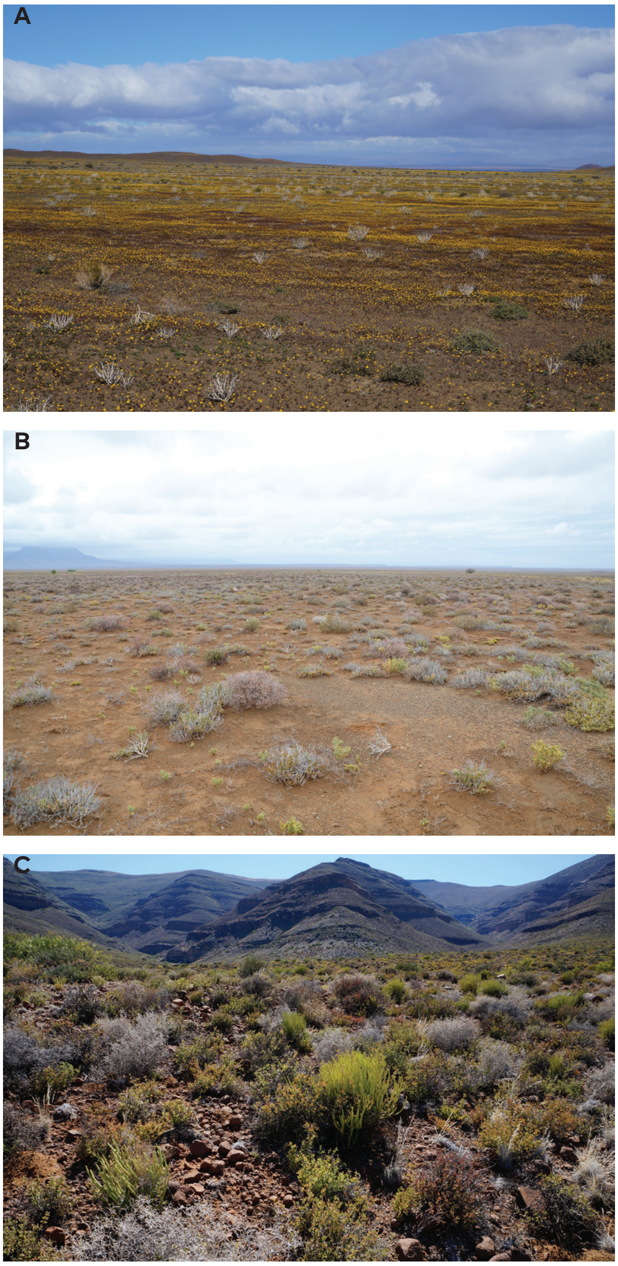

Figure 2. Representative photos of the studied vegetation in the Tankwa Karoo National Park. Photo A shows the landscape and some plants species that are found in the Tanqua Karoo vegetation type. Photo B illustrates the abundance of grasses in Tanqua Wash Riviere vegetation and photo C shows the shrubiness of the Tanqua escarpment vegetation.

Data analysis

A Landsat scene (Landsat-8 OLI/TIRS) captured in September 2015 with a spatial resolution of 30 m was used to extract the NDVI, which was used as a proxy for vegetation cover. This Landsat image was atmospherically and radiometrically corrected for surface reflectance. Based on the NDVI values ranging from -1 to 1, the survey sites in each of the vegetation types were selected to ensure that sites with a range of vegetation cover were included in the field surveys. The data collected during the field surveys was analysed for differences between and among the three vegetation types using two statistical software packages: IBM SPSS version 26 and Primer version 6.

Currently accepted scientific names at the specific, generic, and family levels were updated according to the latest checklist of the Plants of Southern Africa Checklist (South African National Biodiversity Institute 2016). Plant species were grouped according to their families, and into four different life forms encountered at the survey sites (Suppl. material 1).

To assess vegetation structure and floristic composition, we analysed vegetation cover, species richness, diversity (using Shannon–Wiener diversity index) and evenness. The dominance of plant life forms and species was determined using canopy percentage cover. The data were tested for normality using the Shapiro-Wilk before variation analyses were performed. Significant differences ($p<0.05$) amongst the vegetation types across all of the examined parameters were explored using a one-way analysis of variance (ANOVA), thereafter the Tukey HSD post hoc test was used. Furthermore, all the vegetation and environmental variables were subjected to a principal component analysis (PCA) and principal co-ordinate analysis (PCo-A) to investigate any significant associations or possible clustering of survey sites (Zuur et al. 2007). The non-metric multidimensional scaling (NMDS) ordination was produced by applying multiple runs followed by the stability and stress standards described in detail by McCune and Grace (2002). Similarity between the survey sites based on the obtained data was analysed using agglomerative hierarchical clustering after square root transformation.

Results

The survey sites spread throughout the three vegetation types (TK, TWR, and TES) in the TKNP spanned a wide range of elevations that varied between 338 m above sea level on the flatter plains to 1149 m on the escarpment. Slope inclination ranged from zero on the plains to about 40% at some sites on the escarpment. A total number of 150 vascular plant species belonging to 83 genera and 29 families were identified along the transects across all sites (Suppl. material 1). About 86% of the species were dicotyledons, and 14% were monocotyledons. The low proportion of grasses in the park apart from small sandy pockets on the flat open plains is noteworthy. In TK there were 67 species belonging to 48 genera and 18 families, while in TWR, 63 species belonged to 43 genera and 16 families, and in TES, 96 species belonged to 61 genera and 26 families with some of these species shared amongst the three vegetation types.

The vegetation structure of the study area was comprised mainly of shrubs and dwarf shrubs with a high proportion of leaf and stem succulent species. Annuals (therophytes) and cryptophytes were comprised mostly of winter growing species and were abundant after good rains. The study demonstrated that annual plant species were well represented in the open plains and their cover proportion was relatively high (33%), and were less frequent on the escarpment (12%), where perennial shrubs dominated. The most frequently occurring species on the open plains (TK) were *Ursinia nana*, *Euryops annuus*, and *Stipagrostis ciliata* (Table 1, with a detailed list of phytosociological information of the plant species shown in Suppl. material 2). Flood plains (TWR) were dominated by *Drosanthemum framesii*, *Salsola aphylla*, and *Galenia sarcophylla*. The most common species in the escarpment (TES) were *Montinia caryophyllacea*, *Pteronia pallens* and *Tylecodon wallichii*. Small tree species recorded in TES were *M. caryophyllaceae* and *Searsia undulata*. Long-lived trees such as *Vachellia karroo* were confined to rivers and watercourses.

Table 1. Synoptic table showing the species with >35 phi coefficient of association fidelity values in the three main vegetation types TK (Tanqua Karoo), TWR (Tanqua Wash Riviere) and TES (Tanqua Escarpment Shrubland) in Tankwa Karoo National Park. The detailed phytosociological information is shown in Suppl. material 2.

Vegetation type	**TES**	**TWR**	**TK**
Number of relevés	**13**	**15**	**15**
Montinia caryophyllacea Thunb.	66.1	–	–
Pteronia pallens L.f.	66	–	–
Tylecodon wallichii (Harv.) Toelken	65.5	–	–
Drosanthemum lique (N.E.Br.) Schwantes	63.2	6.3	–
Euphorbia mauritanica L.	60.3	–	–
Tenaxia stricta (Schrad.) Conert	54.2	–	–
Tylecodon paniculatus (L.f.) Toelken	54.2	–	–
Justicia cuneata Vahl.	54.2	–	–
Searsia undulata (Jacq.) T.S.Yi	53		
Mesembryanthemum noctiflorum (L.) Schwantes	50	40	–
Oxalis pes-caprae L.	49.9	–	–
Lacomucinaea lineata L.f.	47.8	–	–
Pentzia incana (Thunb.) Kuntze	47.8	–	–
Pteronia incana (Burm.) DC.	47.8	–	–
Tylecodon reticulatus (L.f.) Toelken	47.8	–	–
Berkheya spinosa (L.f.) Druce.	46.3	–	–
Eriocephalus microphyllus DC.	46.3	–	–
Ruschia centrocapsula H.E.K.Hartmann & Stüber	41.4	9.2	–
Asparagus capensis L.	41.1	–	–
Euphorbia rhombifolia E.Mey	41.1	–	–
Crassula muscosa L.	40.8	–	–
Eriocephalus punctulatus DC.	40.8	–	–
Fingerhuthia africana Lehm.	40.8	–	–
Gorteria alienata (Thunb.) Druce	40.8	–	–
Oxalis sp	38.6	–	–
Galenia africana L.	37.3	–	–
Drosanthemum framesii L. Bolus	–	65.8	–
Salsola aphylla L.f.	–	59.3	2.7
Galenia sarcophylla Fenzl	–	56	–
Dimorphotheca pinnata (Thunb.) Norl. v	–	55.5	–
Cotula microglossa (DC.) O.Hoffm. & Kuntze ex Kunt	–	53.4	–
Mesembryanthemum guerichianum Pax	–	50	–
Atriplex lindleyi Moq.	–	44.2	–
Lampranthus otzenianus (Dinter) Friedrich	–	44.2	–
Mesembryanthemum junceum (Haw.) Schwantes	–	41.6	–
Oncosiphon suffruticosum (L.) Källersjö	–	37.8	–
Pteronia villosa L.f.	–	37.8	–
Ursinia nana DC.	–	–	50
Euryops annuus Compton	–	–	47.7
Stipagrostis ciliata (Desf.) De Winter var. capens	–	–	40.8
Gazania lichtensteinii Less.	–	12.2	40.6
Leysera tenella DC.	–	–	37.8
Tetraena chrysopteros Retief	–	–	36.3
Malephora crassa (L.Bolus) H.Jacobsen & Schwantes	–	–	35.4

Table 2. The most common plant families per vegetation type, percentage cover of species per family, and percentage of sites in which families were found for TK (Tanqua Karoo), TWR (Tanqua Wash Riviere) and TES (Tanqua Escarpment Shrubland) in the Tankwa Karoo National Park.

Family	TK		TWR		TES	
	Species (%)	Sites (%)	Species (%)	Sites (%)	Species (%)	Sites (%)
Aizoaceae	26.9	100.0	28.6	100.0	18.8	100.0
Amaranthaceae	4.5	62.5	3.2	85.7	1.0	7.7
Asteraceae	28.4	93.8	28.6	92.9	24.0	100.0
Asparagaceae	0.0	0.0	0.0	0.0	3.1	46.2
Crassulaceae	0.0	0.0	0.0	0.0	5.2	100.0
Euphorbiaceae	0.0	0.0	0.0	0.0	3.1	61.5
Fabaceae	0.0	0.0	4.8	35.7	6.3	38.5
Hyacinthaceae	0.0	0.0	3.2	14.3	0.0	0.0
Geraniaceae	0.0	0.0	0.0	0.0	3.1	38.5
Iridaceae	7.5	100.0	6.3	100.0	2.1	92.3
Malvaceae	0.0	0.0	0.0	0.0	3.1	23.1
Poaceae	7.5	62.5	3.2	21.4	5.2	61.5
Oxalidaceae	3.0	25.0	7.9	42.9	5.2	92.3
Solanaceae	3.0	31.3	1.6	14.3	2.1	53.8
Zygophyllaceae	4.5	87.5	3.2	64.3	3.1	38.5
Other	14.9	43.8	9.5	50.0	14.6	92.3

Table 3. The mean values, standard error and the analysis of variance (one-way) for the examined parameters in the surveyed vegetation types. The superscripts indicate the significant differences amongst the vegetation types escarpment (TES), flood plains (TWR), and open flat plains (TK) in the various examined parameters. The asterisks demonstrate the significant differences amongst the parameters within each vegetation type.

Vegetation type	TK		TWR		TES		*F* value amongst vegetation types	*p*-value amongst vegetation types
Number of sampling sites	15		15		13			
	Mean	SE	Mean	SE	Mean	SE		
Elevation (m a.s.l.)	411.60^{a}	15.03	511.73^{b}	20.82	786.62^{c}	47.36	42.306	0.000
Slope (%)	1.33^{a}	0.39	2.73^{a}	0.80	15.77^{b}	2.71	26.299	0.000
Annual cover (%)	35.77^{a}	2.71	18.28^{b}	2.03	11.69^{c}	2.99	23.351	0.000
Perennial cover (%)	8.62^{a} *	1.74	29.40^{b} *	3.38	49.94^{c}	3.16	51.858	0.000
Litter cover (%)	1.03^{a}	0.34	6.43^{b}	1.11	4.92^{b}	0.64	13.251	0.000
Rock cover (%)	0.53^{a}	0.21	1.85^{a}	1.20	15.02^{b}	1.72	45.160	0.000
Denuded areas (%)	54.05^{a}	1.49	44.03^{b}	3.79	18.42^{c} *	3.06	37.528	0.000
Shrub height (m)	0.16^{a}	0.02	0.26^{b}	0.02	0.43^{c} *	0.03	33.383	0.000
Succulent (%)	17.68^{a}	5.33	38.27^{b}	3.90	27.99$^{a, b}$	4.88	4.937	0.012
Nano-phanerophyte spp. (%)	0.54^{a}	0.24	0.42^{a}	0.31	4.10^{b}	1.24	8.902	0.001
Chamaephyte spp. (%)	50.70^{a} **	6.78	68.21$^{a, b}$	4.39	75.79^{b}	5.39	5.179	0.010
Cryptophyte spp. (%)	22.76^{a}	5.32	15.57^{b}	2.98	16.76^{c}	4.18	0.836	0.441
Therophyte spp. (%)	26.00^{a}	6.52	17.90$^{a, b}$	5.05	3.32^{b}	1.31	5.010	0.011
Species richness (S)	10.33^{a}	0.51	16.47^{b}	1.15	22.08^{c}	2.06	19.495	0.000
Shannon-Wiener index (H′)	1.46^{a}	0.09	2.00^{b}	0.14	2.16^{b}	0.14	8.706	0.001
Species evenness (E)	0.63^{a}	0.03	0.77^{b}	0.01	0.70$^{a, b}$	0.03	7.602	0.002

*** The mean difference amongst the parameters within each vegetation type is significant at the 0.001 level.
** The mean difference amongst the parameters within each vegetation type is significant at the 0.01 level.
* The mean difference amongst the parameters within each vegetation type is significant at the 0.05 level.

The most common families in all the surveyed vegetation types were *Aizoaceae*, *Iridaceae*, and *Asteraceae*. *Amaranthaceae* and *Zygophyllaceae* were more common in TK and TWR while Fabaceae was only observed in TWR and TES. *Poaceae* was more frequent in TK and TES than in TWR. *Oxalidaceae* and *Solanaceae* were more frequent in TES than in TK and TWR. *Asparagaceae*, *Crassulaceae*, *Euphorbiaceae*, *Geraniaceae*, and *Malvaceae* were only recorded on the escarpment (Table 2).

The mean perennial vegetation cover was 28% across all the study sites and was significantly different amongst the vegetation types. Perennial vegetation was sparser in the TK (9%) and TWR (29%) and was significantly higher in the TES (50%) (Table 3). Low vegetation cover was associated with high mean values for denuded areas and a higher annual cover (Table 3). The mean shrub height value was 0.27 m and showed a significant difference amongst the vegetation types (Table 3).

The results showed a low rock cover (mean 5%) with the mean rock cover lowest for both TWR and TK and highest in TES. The mean litter cover was also low (4%), with the most litter found in the TWR vegetation and least litter cover (1%) in the TK (Table 3).

The most dominant life forms were chamaephytes, which comprised 64% of the species, cryptophytes (geophytes) 18%, therophytes 16%, and nano-phanerophytes 2%. Chamaephytes dominated the TES while, therophytes were most abundant in the TK as were the Cryptophytes (Table 3). The nano-phanerophytes were represented by only a few species (e.g. *Lycium cinereum*. *Searsia undulata*

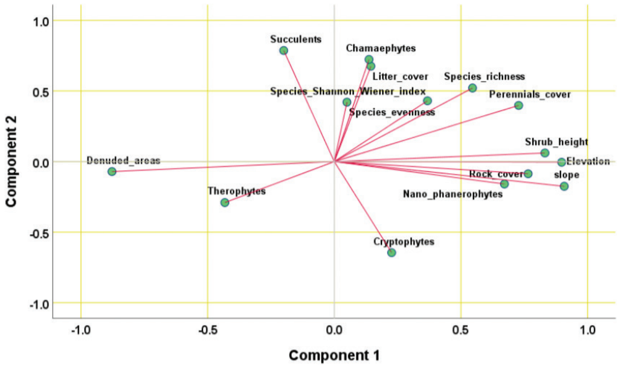

Figure 3. Bi-plot of the Principal Component Analysis (PCA) showing the distribution of the examined variables according to the first two Principal Components (PCs), the lines meet at the (0, 0) and represent the original variables. The angle between the arrows of a pair of variables indicated similarity in the distribution of the variables. The eigenvalue of the first PC axis was 6.252 explaining 42% of the variation while the eigenvalue for the second PC axis was 2.377 explaining 16% of the variation.

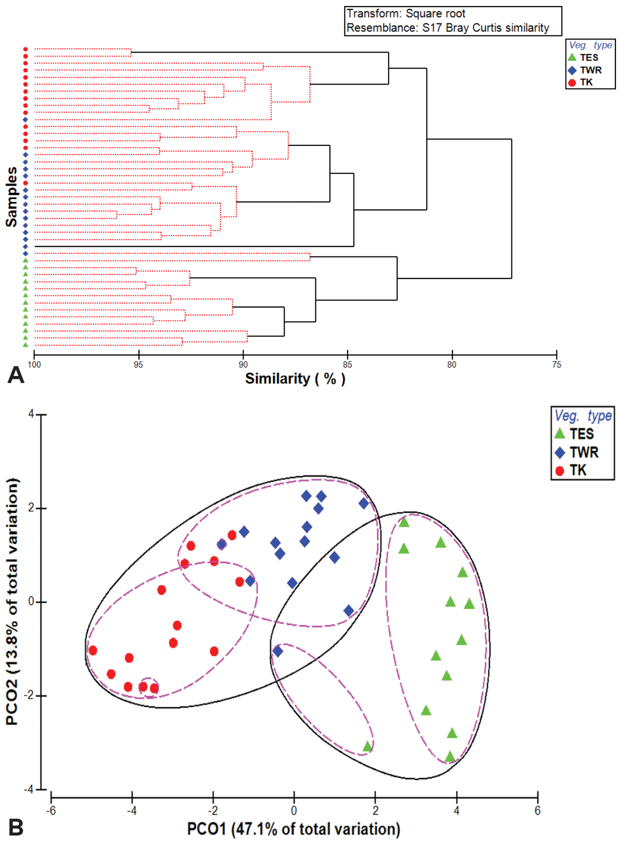

Figure 4. (A) Clustering diagram of Bray-Curtis similarity amongst the survey sites in the different vegetation types; Tanqua Karoo (TK), Tanqua Wash Riviere (TWR), and Tanqua Escarpment Shrubland (TES) based on the life-form and environmental variables examined during this study), **(B)** Principal Co-ordinate Bi-plot for the distribution of the survey sites based on the different species, life-form and environmental variables, the first two axes explain 61% of the variation. The eigenvalue along the first axis was 336.08 and captured 47% of the total variation. Along the second axis, the eigenvalue was 98.284 and captured 14% of the total variation. The solid black lines denote an 80% similarity between sites wheres the purple broken lines denote a 85% similarity.

and *Montinia caryophyllacea*) with the highest percentage cover in the TES (Table 3).

The mean species richness (S) was 16 species, mean Shannon-Wiener index (H') 1.86 and species evenness (E) 0.7. The highest mean species richness and Shannon-Wiener index (H') were recorded in the TES and the lowest in the TK (Table 3).

The principal component analysis (PCA) showed that the first two PC axes explained 58% of the total variation amongst the examined variables (Figure 3). The first axis was positively related to slope, elevation, rock cover, perennial cover, shrub height, nano-phanerophytes, and negatively related to denuded areas and therophytes. The second axis was positively related to evenness, Shannon-Wiener index, litter cover, species richness, succulent species, chamaephytes, and negatively related to cryptophytes (Figure 3).

The cluster analysis of the survey sites based on the variables listed in Table 3, demonstrated a clear association amongst the TES survey sites. However, there was interference between the TWR and the TK in a few sites. The Bray-Curtis similarity at 80% categorised the survey sites into two main groups and at 85% similarity into six sub-groups (Figure 4A). The ordination using principal coordinate analysis (PCo-A) showed that the first and second axes explain 61% of the total variation amongst the survey sites. The eigenvalue along the first axis was 336.08 and explained 47% of the total variation. Along the second axis, the eigenvalue was 98.284 and explained 14% of the total variation (Figure 4B).

Discussion

Elevation has been shown to be a key factor in determining the distribution of plant species and vegetation communities in different landscapes (Hegazy et al. 2011; Piers et al. 2019). This is due to the effect of elevation on climatic variables such as temperature and precipitation (Xu et al. 2018), soil nutrient and water infiltration status (Petersen et al. 2004) but also the role elevation plays in grazing distribution (Samuels et al. 2007, 2022). Isohyets from meteorological records (2006–2014) for the study area shows aridity increases from the eastern uplands of the Roggeveld Mountains to the western low relief plains. In this context, some previous studies indicated that the temporal and spatial fluctuations in climatic factors enhance the variation of the vegetation in sensitive arid ecosystems mainly due to elevation variation (Roux and Vorster 1983; Chapin 2003).

The percentage cover values obtained for the denuded areas were significantly higher for the plains (TK and TWR) than in the escarpment (TES) (Table 3). This may be a result of the relatively higher aridity and decades of overgrazing in preferred habitats such as on plains and flatlands in general in comparison to the elevated and steeply sloped landscapes that are mostly used during drought periods as stated in previous studies (Bester et al. 2012; Steyn et al. 2013; Saaed et al. 2022b; Samuels et al. 2007, 2016). The similarity in denuded area cover between TK and TWR was also supported by the clustering of these two vegetation types on the lowlands. Larger denuded areas were associated with low soil cover (i.e., litter and rock), particularly on the open plains. Litter cover in many sites was completely absent due to the low standing vegetation cover (Saaed et al. 2022b), which is typical of arid regions. The low surface litter may lead to an increase in the evaporation rate from the soil, lower organic material and nutrient contents retained and recycled in the soil (Tongway and Hindley 2003), and higher degradation potential of these areas by decreasing soil stability and increasing soil erosion through agents such as wind and water (Saaed et al. 2022a).

This study illustrated that each vegetation type in the study area has adapted to its local environmental conditions which determines its characteristic structure and floristic composition. The vegetation cover and species diversity on the escarpment slopes were higher, as a result of a mixture of succulent and woody, long-lived non-succulent shrubs, in comparison to the plains dominated by therophytes and cryptophytes. This turnover of species across the Tanqua landscape has also been found in the Richtersveld, which is believed to be driven primarily by climatic factors and local habitat features, i.e., elevation, slope, and soil cover (Jürgens et al. 1999). In this part of the Tanqua Karoo, the elevational gradient and its associated effects on microclimates such as rock cover and slope as noted in Figure 3 is a crucial influential environmental factor affecting plant community composition.

Throughout the study area, the most common families were *Aizoaceae*, *Iridaceae*, and *Asteraceae* (Table 2), which support earlier work of Steyn et al. (2013). These authors generated a comprehensive species list using herbarium specimens (lodged in herbaria over decades/centuries) and active collecting expeditions to collect every species found across the park. Previous studies within the broader Succulent Karoo (e.g., Gibbs-Russell 1987; Milton et al. 1997; Schmiedel and Jürgens 1999; Ellis et al. 2006) reported similar findings. The abundance of these particular families may reflect the aridity prevailing in the area, since these families are generally more common in arid habitats (Sayed 1998).

The distributions of some plant families in the study area were restricted to particular habitats. *Asparagaceae*, *Crassulaceae*, *Euphorbiaceae*, *Geraniaceae*, and *Malvaceae* were only recorded on the escarpment. The geology, soils and microclimates of the escarpment may be more favourable to species in these families. Studies (e.g. Anderson et al. 2010) have shown that geology and soils play a major influence on the distribution of plant families. *Zygophyllaceae* and *Amaranthaceae* were more frequent in the open and on flood plains as some of these species seem to prefer disturbed, more saline, areas often found on the plains. This is in contrast to other perennial shrubs in the *Zygophyllaceae* family that are not indicators of disturbance. This study also observed that *Atriplex lindleyi* (*Amaranthaceae*), a naturalised dwarf shrub from Australia was present on the plains in the TKNP. *Fabaceae* species were common on the escarpment and very low in the open plains. The very low contribution of the *Fabaceae* in the plains contrasts with the finding of Gibbs-Russell (1987) who stated that this family is frequent in the Succulent Karoo biome. This may be a result of the long grazing history (Driver et al. 2002; Saaed et al. 2022b) since the *Fabaceae* species are highly palatable and nutritious forage species (Shavanov 2021).

Generally, the perennial plant cover throughout the study area was low. The lower perennial and higher annual cover, particularly on the plains, is evidence of low productivity and substantial vegetation degradation (Anderson and Hoffman 2007). Distinguished from other areas in the Succulent Karoo region (Born et al. 2007), the low proportion of grasses in the study area is also a sign of the poor health status of the rangeland. In such degraded rangelands in other parts of the Succulent Karoo, exposure to continuous overgrazing for decades resulted in a decline of the palatable shrubs and perennial grasses (Anderson and Hoffman 2007; Desmet 2007), in addition to the negative impact of inappropriate stocking rates on species richness.

As a consequence of the higher precipitation and lower temperature and evapotranspiration rate as well as reduced grazing densities, the escarpment is characterised by denser and taller shrubs, with the presence of some small trees. This contrasts with the low open plains characterised by a sparse cover of dwarf shrubs and numerous annual species which are promoted by heavy grazing and are strongly dependent on rainfall (Anderson and Hoffman 2007).

Even though there was a significant difference amongst the vegetation types in terms of cover of succulent species (leaf and stem), the succulent species contribution was notably high in all of the vegetation types. This high abundance of succulent species is common throughout the Tanqua Karoo region (Van der Merwe and Van Rooyen 2011b). In this study the common succulent species included *Augea capensis*, *Drosanthemum lique*, and *Malephora crassa*. Many of these succulent shrubs are shallow-rooted and mortality amongst this guild is high during severe droughts (Von Willert et al. 1992; Jürgens et al. 1999) resulting in a high turnover of plants in the area. This finding of generally high succulent abundance in the TKNP was also confirmed by Saaed et al. (2022b).

Different plant life forms are usually distributed along an elevational gradient (Whittaker 1960; He and Chen 1997). The most dominant life form in the study area was the chamaephyte group, which comprised 64% of the species. On the plains, chamaephytes were co-dominated by therophyte and cryptophyte species. On the escarpment, chamaephytes were co-dominated by cryptophyte species, which corresponds with the findings of Van der Merwe and Van Rooyen (2011a). Thus, the escarpment is less dynamic when compared to the open plains due to the higher contribution of chamaephytes and nano-phanerophytes, which have a longer life span when compared to the plains where therophytes and cryptophytes have higher abundance. In the plains, the periodically high contribution of cryptophytes and therophytes is strongly coupled with rainfall seasonality and events and their dominance is consistent with what may be expected in an arid climate (Van der Merwe and Van Rooyen 2011a; Van Rooyen et al. 2015, Van Rooyen et al. 2018). The significant variation in life form structure in the TKNP, particularly in chamaephyte, therophyte and cryptophyte cover across the vegetation types, provides additional evidence of indigenous vegetation structure driven by environmental factors. Vegetation structure is an important variable for monitoring complex changes in disturbed ecosystems where changes related to rangeland degradation can be detected and described (Hegazy et al. 2011; Hanke et al. 2014).

The variation in vegetation composition is reflected in the biodiversity patterns, which also varied spatially across the study area, with higher biodiversity values found for the escarpment. Species richness on the escarpment was about double the species richness on the open plains and about 1.6 times greater than on the flood plains. The Shannon-Wiener index showed a similar trend, while there was a relatively high species evenness index across the vegetation types. These plant diversity patterns may be attributed to the variation in the environmental factors (e.g. elevation gradient, rainfall, air temperature), which create a variety of habitats with different environmental conditions (Zhao et al. 2005; Hegazy et al. 2011). Elevation is amongst the most important environmental factors that influence biodiversity distribution across a landscape (Bhat et al. 2020). Plant species diversity is affected by the large scale and micro patterns of moisture and temperature conditions that usually change along an elevational gradient (Zhao et al. 2005). The high evenness scores may be related to a breakdown of hierarchical dominance and competitive structures with greater disturbance across the park (Rutherford and Powrie 2010). In addition to the variation in abiotic factors across the different elevations, the stresses caused by the past overgrazing and cropping disturbances particularly on the plains would have significantly influenced species richness and diversity.

There were significant variations amongst the surveyed sites within the same vegetation types in many of the examined parameters such as vegetation cover, litter cover, denuded areas, succulent species, species richness, and diversity illustrating variability within the same vegetation type. This may indicate different states of vegetation condition and different degradation potentials within the same vegetation type. The finer differences in soils, microclimates and plant-plant and plant-animal interactions have been shown to also play a role in variability within arid landscapes such as in the case of heuweltjies (termitaria) and quartz patches specifically in the Succulent Karoo (Kunz et al. 2012; Schmiedel et al. 2015; Eibes et al. 2021).

Although the vegetation differences amongst the vegetation types are likely a result of an interaction of the biotic and abiotic components of the system, the results of a principal component analysis (PCA) (Figure 4) demonstrated the particularly high influence of elevation on vegetation characteristics. The large influence of elevation on vegetation cover, productivity, distribution, and composition in the area is most likely through its influence on the edaphic and microclimatic factors. However other variables, such as slope and rock cover, also contribute to variability. This corresponds with the findings of other studies elsewhere, where small fluctuations in environmental parameters were shown to lead to relatively large shifts in vegetation states (Körner 2003; Stage and Salas 2007; Anderson et al. 2010; Hegazy et al. 2011).

Conclusion

This study revealed the high heterogeneity in vegetation structure and composition and their related indices that included cover, plant height, species richness and diversity and life form diversity across the Tankwa Karoo National Park. Areas in the park located at higher elevations where TES vegetation prevails, were more vegetated and species rich due to the effect of elevation and topography on climate and habitat heterogeneity. The low-lying TK was more arid and environmentally stressed and exhibited a low vegetation and litter cover. The effect of elevation on vegetation characteristics improves our understanding of the likely trajectories of change in vegetation when the climate changes in the future. Concomitantly, this information could be used to prioritise areas for active interventions such as degraded areas which have significantly lower plant cover and diversity, and are therefore more susceptible to erosion and further degradation. Personal observations by the authors noted that some restoration interventions by the state have been hugely successful in the park thus results of this study can also be used to inform those interventions.

Data availability

The data would be made available by the authors on reasonable request.

Author contributions

M.I.S. conceived the study, analyzed the data, authored and reviewed the manuscript and approved the final draft. M.S. conceived the study, analyzed the data, authored and reviewed the manuscript and approved the final draft.

S.J.J. conceived and designed the experiments, reviewed the drafts of the manuscript. M.L.M. conceived study, authored and reviewed drafts of the manuscript and approved the final draft. H.v.d.M. assisted with plant identification, authored and reviewed the manuscript and approved the final draft. L. K. conceived and designed the experiments, analyzed the data, prepared figures and tables, reviewed drafts of the manuscript and approved the final draft.

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References

Anderson PML, Hoffman MT (2007) The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. Journal of Arid Environments 70: 686-700. https://doi.org/10.1016/j.jaridenv.2006.05.017

Anderson PML, Hoffman MT, O'Farrell PJ (2010) Above ground perennial plant biomass across an altitudinal and land-use gradient in Namaqualand, South Africa. South African Journal of Botany 76: 471–481. https://doi.org/10.1016/j.sajb.2010.03.004

Bester SP, Stoffel P, Klopper RR, Steyn HM, Bezuidenhout H (2012) New plant records for Tankwa Karoo National Park, South Africa. Koedoe 54: 1–9. https://doi.org/10.4102/koedoe.v54i1.1066

Beukes PC, Ellis F (2003) Soil and vegetation changes across a Succulent Karoo grazing gradient. African Journal of Range and Forage Science 20: 11–19. https://doi.org/10.2989/10220110309485793

Bhat JA, Kumar M, Negi AK, Todaria NP, Malik ZA, Pala NA, Kumar A, Shukla G (2020) Altitudinal gradient of species diversity and community of woody vegetation in the Western Himalayas. Global Ecology and Conservation 24: e01302. https://doi.org/10.1016/j.gecco.2020.e01302

Born J, Linder HP, Desmet P (2007) The Greater Cape Floristic Region. Journal of Biogeography 34: 147–162. https://doi.org/10.1111/j.1365-2699.2006.01595.x

Chapin FS (2003) Effects of plant traits on the ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. Annals of Botany 91: 455–463. https://doi.org/10.1093/aob/mcg041

Cowling RM, Gibbs-Russel GE, Hoffman MT, Hilton-Taylor C (1989) Patterns of plant species diversity in southern Africa. In: Huntley BJ (Ed.) Biotic diversity in southern Africa: Concepts and conservation. Oxford University Press, Cape Town, ZA, 19–50.

Cowling RM, Hilton-Taylor C (1994) Patterns of plant diversity and endemism in southern Africa: an overview. In: Huntley BJ (Ed.) Botanical Diversity in Southern Africa. Pretoria, South Africa: National Botanical Institute. Strelitzia 1: 31–52.

Desmet PG (2007) Namaqualand, A brief overview of the physical and floristic environment. Journal of Arid Environments 70: 570–587. https://doi.org/10.1016/j.jaridenv.2006.11.019

Driver A, Maze K, Cowling RM (2002) The Succulent Karoo Ecosystem Plan (SKEP). Botanical Society of South Africa, Kirstenbosch, ZA.

Du Toit PCV (1997) Description of a method for assessing veld condition in the Karoo. African Journal of Range and Forage Science 14: 90–93. https://doi.org/10.1080/10220119.1997.9647928

Eibes PM, Oldeland J, Irl SDH, Twerski A, Kühne N, Schmiedel U (2021) Partitioned beta diversity patterns of plants across sharp and distinct boundaries of quartz habitat islands. Journal of Vegetation Science 32: e13036. https://doi.org/10.1111/jvs.13036

Ellis AG, Weis AE, Gaut BS (2006) Evolutionary radiation of "stone plants" in the genus *Argyroderma* (*Aizoaceae*): unravelling the effects of landscape, habitat, and flowering time. Evolution 60: 39–55. https://doi.org/10.1111/j.0014-3820.2006.tb01080.x

Francis ML, Fey MV, Prinsloo HP, Ellis F, Mills AJ, Medinski TV (2007) Soils of Namaqualand: Compensations for aridity. Journal of Arid Environments 70: 588–603. https://doi.org/10.1016/j.jaridenv.2006.12.028

Gibbs-Russell GE (1987) Preliminary floristic analysis of the major biomes in southern Africa. Bothalia 17: 213–227. https://doi.org/10.4102/abc.v17i2.1038

Hanke W, Böhner J, Dreber N, Jürgens N, Schmiedel U, Wesuls D, Dengler J (2014) The impact of livestock grazing on plant diversity: An analysis across dryland ecosystems and scales in southern Africa. Ecological Applications 24: 1188–1203. https://doi.org/10.1890/13-0377.1

He JS, Chen W (1997) A review of gradient changes in species diversity of land plant communities. Acta Ecologica Sinica 17: 91–99.

Hegazy AK, Boulos L, Kabiel HF, Sharashy OS (2011) Vegetation and species altitudinal distribution in Al-Jabal Al-Akhdar landscape, Libya. Pakistan Journal of Botany 43: 1885–1898.

Hoffman T, Ashwell A (2001) Nature divided: land degradation in South Africa. 1st ed. University of Cape Town Press, Cape Town, ZA, 176 pp.

Hoffman MT, Cousins B, Meyer T, Peterson A, Hendricks H (2009) Historical and contemporary land use and the desertification of the Karoo. In: Dean WRJ, Milton SJ (Eds) The Karoo: Ecological patterns and processes. Cambridge University Press Cambridge, UK, 257–273. https://doi.org/10.1017/CBO9780511541988.022

Jürgens N, Gotzmann IH, Cowling RM (1999) Remarkable medium-term dynamics of leaf succulent *Mesembryanthemaceae* shrubs in the winter-rainfall desert of northwestern Namaqualand, South Africa. Plant Ecology 142: 87–96. https://doi.org/10.1023/A:1009862025821

Körner C (2003) Alpine plant life functional plant ecology of high mountain ecosystems. 2nd ed. Springer, New York, US, 349 pp.

Kraaij T, Milton SJ (2006) Vegetation changes (1995–2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. Journal of Arid Environments 64: 174–192. https://doi.org/10.1016/j.jaridenv.2005.04.009

Kunz NS, Hoffman MT, Weber B (2012) Effects of heuweltjies and utilization on vegetation patterns in the Succulent Karoo, South Africa. Journal of Arid Environments 87: 198–205. https://doi.org/10.1016/j.jaridenv.2012.05.007

Land Type Survey staff (2010) Land types of the map 3220 Sutherland. Memoirs on the Agricultural Natural Resources of South Africa No. 36. ARC-Institute for Soil, Climate and Water, Pretoria, ZA.

Land Type Survey staff (2012) Land types of the maps 3118 Calvinia and 3218 Clanwilliam. Memoirs on the Agricultural Natural Resources of South Africa No. 30. ARC-Institute for Soil, Climate and Water, Pretoria, ZA.

Li D (2018) The Plant Functional Traits of Arid and Semiarid Grassland Plants under Warming and Precipitation Change. In: Ratnadewi D, Hamim H (Eds) Plant Growth and Regulation - Alterations to Sustain Unfavorable Conditions. IntechOpen, London, UK. https://doi.org/10.5772/intechopen.79744

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, US, 304 pp.

Milton SJ, Yeaton RI, Dean WRJ, Vlok JHJ (1997) Succulent Karoo. In: Cowling RM, Richardson DM, Pierre SM (Eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, UK, 131–166.

Milton SJ, Dean WRJ (1995) South Africa's arid and semiarid rangelands: why are they changing and can they be restored? Environmental Monitoring and Assessment 37: 245–264. https://doi.org/10.1007/978-94-009-1635-7_18

Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca GAB (2004) Hotspots Revisited. 1st ed. Cemex, Mexico City, MX, 392 pp.

Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho, and Swaziland [Strelitzia 19]. South African National Biodiversity Institute, Pretoria, ZE.

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. JohnWiley & Sons, New York, US, 547 pp.

Osman R, Masubelele ML, Khomo L, Chimphango S (2019) Soil and vegetation differences across ecological boundaries in an arid South African ecosystem. African Journal of Ecology 57: 344–352. https://doi.org/10.1111/aje.12612

Palmer AR, Hoffman MT (1997) Nama-Karoo. In: Cowling RM, Richardson DM, Pierce SM (Eds) Vegetation of Southern Africa. 1st ed. Cambridge University Press, Cambridge, UK, 167–188.

Palmer T, Ainslie A (2006) Country Pasture/Forage Resource Profiles: South Africa. FAO, Rome, IT.

Petersen A, Young EM, Hoffman MT, Wynn-Jones GE, Musil CF (2004) The impact of livestock grazing on landscape biophysical attributes in privately and communally managed rangelands in Namaqualand. South African Journal of Botany 70: 777–783. https://doi.org/10.1016/S0254-6299(15)30179-4

Piers LC, Samuels MI, Masubelele ML, Khomo L (2019) Inselbergs persist as islands of diversity in a heavily grazed rangeland mosaic at the nexus of three arid biomes. African Journal of Range and Forage Science 36: 125–128. https://doi.org/10.2989/10220119.2019.1568302

Raunkiær CC (1934) The life forms of plants and statistical plant geography: being the collected papers of Raunkiær C, translated by Gilbert-Carter H, Fausbøll A., Tansley AG. Introduction by Tansley AG. Oxford University Press, Oxford, UK.

Roux PW, Vorster M (1983) Vegetation change in the Karoo. Proceedings of the Grassland Society of Southern Africa 18: 25–29. https://doi.org/10.1080/00725560.1983.9648976

Rubin F (1998) The physical environment and major plant communities of the Tankwa Karoo National Park. Koedoe 41: 61–94. https://doi.org/10.4102/koedoe.v41i2.253

Rutherford MC, Powrie LW (2010) Severely degraded rangeland: Implications for plant diversity from a case study in Succulent Karoo, South Africa. Journal of Arid Environments 74: 692–701. https://doi.org/10.1016/j.jaridenv.2009.10.013

Saaed, MWB (2018) Assessment of degradation and prospects of rehabilitation of the arid rangelands in the Tanqua Karoo region, South Africa, Tankwa Karoo National Park as a case study. Ph.D. thesis, Stellenbosch University, Stellenbosch, ZA.

Saaed, MWB, Jacobs SJ, Masubelele ML, Samuels, MI, Munch Z, Khomo LM, El-barasi YM (2018) The composition of the soil seedbank and its role in ecosystem dynamics and rehabilitation potential in the arid Tankwa Karoo Region, South Africa. African Journal of Range and Forage Science 35: 351–361. https://doi.org/10.2989/10220119.2018.1526824

Saaed, MWB, Jacobs SJ, Masubelele ML, Samuels, MI, Munch Z, Khomo LM (2020) Fifteen-year resilience against further degradation of Succulent Karoo vegetation in South Africa, Journal of Arid Environments 178: 104–152. https://doi.org/10.1016/j.jaridenv.2020.104152

Saaed MWB, Jacobs SJ, Masubelele ML, Samuels MI, Khomo LM (2022a) Does the landscape functionality approach provide insight into rangeland conditions? A case study in the Tanqua Karoo region, South Africa. PeerJ 10: e13305. https://doi.org/10.7717/peerj.13305

Saaed MWB, Jacobs SJ, Masubelele ML, Samuels MI, Khomo LM (2022b) Imprint of overgrazing on the soil and vegetation of fertility islands in the degraded Succulent Karoo, South Africa. Land Degradation and Development 33: 379–387. https://doi.org/10.1002/ldr.4159

Samuels, MI, Allsopp N, Knight R (2007) Patterns of resource use by livestock during and after drought on the commons of Namaqualand, South Africa. Journal of Arid Environments 70: 728–739. https://doi.org/10.1016/j.jaridenv.2006.11.006

Samuels MI, Allsopp N, Hoffman MT (2022) Stocking density and distribution in relation to vegetation in a biodiverse semi-arid pastoral system in South Africa. The Rangeland Journal 44: 1–12. https://doi.org/10.1071/RJ21046

Samuels I, Cupido C, Swarts MB, Palmer AR, Paulse JW (2016) Feeding ecology of four livestock species under different management in a semi-arid pastoral system in South Africa. African Journal of Range and Forage Science 33: 1–9. https://doi.org/10.2989/10220119.2015.1029972

Sayed OH (1998) Phenomorphology and ecophysiology of desert succulents in eastern Arabia, Journal of Arid Environments 40: 177–189. https://doi.org/10.1006/jare.1998.0434

Schmiedel U, Jürgens N (1999) Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa. Plant Ecology 142: 57–69. https://doi.org/10.1023/A:1009818210799

Schmiedel U, Kühne N, Twerski A, Oldeland J (2015) Small-scale soil patterns drive sharp boundaries between succulent "dwarf" biomes (or habitats) in the arid Succulent Karoo, South Africa. South African Journal of Botany 101: 129–138. https://doi.org/10.1016/j.sajb.2015.05.001

Schulz BK, Bechtold WA, Zarnoch SJ (2009) Sampling and estimation procedures for the vegetation diversity and structure indicator. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-781. https://doi.org/10.2737/PNW-GTR-781

Schulze RE (1997) South African Atlas of Agrohydrology and Climatology. Water Research Commission, Pretoria, ZA.

Shavanov MV (2021) The role of food crops within the *Poaceae* and *Fabaceae* families as nutritional plants. International Conference on World Technological Trends in Agribusiness: Earth and Environmental Science 624: 012111. https://doi.org/10.1088/1755-1315/624/1/012111

Smith GF, Hobson SR, Meyer NL, Chesselet P, Archer RH, Burgoyne PM, Glen HF, Herman PPJ, Retief E, … Welman WG (1993) Southern African succulent plants: an updated synopsis. Aloe 30: 32–74.

South African National Biodiversity Institute (2016) Botanical Database of Southern Africa (BODATSA). [accessed 08 February 2023]

Stage AR, Salas C (2007) Interactions of elevation, aspect, and slope in models of forest species composition and productivity. Forest Science 53: 486–492.

Steyn HM, Bester SP, Bezuidenhout H (2013) An updated plant checklist for Tankwa Karoo National Park, South Africa. South African Journal of Botany 88: 247–251. https://doi.org/10.1016/j.sajb.2013.07.018

Strauss C, de Kock G, Songelwa N, Mabunda D, Dlamin KD (2014) Tankwa Karoo National Park, a draft management plan for stakeholder comment for the period 2014–2024. SANParks, South Africa.

Tongway DJ, Hindley NL (2003) Indicators of ecosystem rehabilitation success: Stage two, verification of EFA indicators, final report.

Van der Merwe H, Bezuidenhout H, Bradshaw PL (2015) Landscape unit concept enabling management of a large conservation area: A case study of Tankwa Karoo National Park, South Africa. South African Journal of Botany 99: 44–53. https://doi.org/10.1016/j.sajb.2015.03.187

Van der Merwe H, Van Rooyen MW (2011a) Life form spectra in the Hantam-Tanqua-Roggeveld, South Africa. South African Journal of Botany 77: 371–380. https://doi.org/10.1016/j.sajb.2010.10.002

Van der Merwe H, Van Rooyen MW (2011b) Species-area relationships in the Hantam-Tanqua-Roggeveld, Succulent Karoo, South Africa. Biodiversity and Conservation 20: 1183–1201. https://doi.org/10.1007/s10531-011-0022-3

Van der Merwe H, Van Rooyen MW, Van Rooyen N (2008) Vegetation of the Hantam Tanqua Roggeveld subregion, South Africa, Part 2: Succulent Karoo Biome related vegetation. Koedoe 50: 160–183. https://doi.org/10.4102/koedoe.v50i1.148

Van Rooyen MW, Le Roux A, Geldenhuys C, Van Rooyen N, Broodryk NL, Van der Merwe H (2015) Long-term vegetation dynamics (40 yr) in the Succulent Karoo, South Africa: Effects of rainfall and grazing. Applied Vegetation Science 18: 311–322. https://doi.org/10.1111/avsc.12150

Van Rooyen MW, Le Roux A, Van der Merwe H, Van Rooyen N, Geldenhuys C (2018) Long-term vegetation change (>20 years) in the plains habitat on the Goegap Nature Reserve, Succulent Karoo, South Africa. African Journal of Range & Forage Science 35: 3–4, 289–302. https://doi.org/10.2989/10220119.2018.1498802

Von Willert DJ, Eller BM, Werger MJA, Brinckmann E, Ihlenfeldt HD (1992) Life strategies of succulents in deserts: With special reference to the Namib Desert. 1st ed. Cambridge University Press, Cambridge, UK, 368 pp.

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279–338. https://doi.org/10.2307/1943563

Xu F, Jia Y, Peng H, Niu C, Liu J (2018). Temperature and precipitation trends and their links with elevation in the Hengduan Mountain region, China. Climate Research 75: 163–180. https://doi.org/10.3354/cr01516

Zhao CM, Chen WL, Tian ZQ, Xie ZQ (2005) Altitudinal pattern of plant species diversity in Shennongjia Mountains, Central China. Journal of Integrative Plant Biology 47: 1431–1449. https://doi.org/10.1111/j.1744-7909.2005.00164.x

Zuur AF, Ieno EN, Smith GM (2007) Analysing Ecological Data. Springer. https://doi.org/10.1007/978-0-387-45972-1

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Supplementary material

Supplementary material 1
A checklist of species and their categorization within the different plant families, growth and life forms in the Tankwa Karoo National Park as identified during the study.
Link: https://doi.org/10.3897/VCS.86310.suppl1

Supplementary material 2
Phytosociological information of plant species in relation to relevés and vegetation types in the Tankwa Karoo National Park.
Link: https://doi.org/10.3897/VCS.86310.suppl2