Vegetation response to grazing and drought (13 yr) in a conservation area in the Succulent Karoo, South Africa

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Abstract

Rangelands of arid ecosystems are driven by internal and external environmental controls. Grazing pressure is an important anthropogenic driver, but stochastic environmental events such as rainfall variability and prolonged drought can have profound effects on arid vegetation. We investigated the effect of a prolonged drought and initial high grazing pressure on range condition, perennial vegetation cover, life form cover, vegetation composition and vegetation diversity at five monitoring sites in a conservation area in arid Succulent Karoo vegetation. The response of the rocky mountainous vegetation to drought and grazing differed notably from the response of the sandy plains vegetation. Range condition and perennial vegetation cover reduced drastically in all habitats, although the extent of deterioration was less in the mountainous habitats. Annual vegetation cover was associated with inter-annual rainfall variability. Of the perennial vegetation diversity indices species richness decreased at three of five sites, whereas species evenness increased at three of five sites. Shannon-Wiener index of diversity and Simpson's diversity index trends were inconsistent. Vegetation composition changed directionally from a quasi-stable state in all five monitoring sites as the drought persisted. The extent of the change was less in mountainous habitats indicating potentially higher resilience than in plains habitats, though grazing pressure was lower in the mountains than on the plains over the study period. The existence of quasi-stable states, together with the observed directional changes in vegetation composition in response to both drought and grazing, indicated that both equilibrium and non-equilibrium vegetation dynamics apply.

Keywords: Directional change; Nonequilibrium theory; Overgrazing; Rainfall; Rangeland condition; Species diversity

Introduction

The Namaqualand region of the Succulent Karoo Biome in western South Africa is an arid system with a diverse biodiversity assemblage of global significance (Cowling et al., 1999). Although the vegetation of the region has evolved to withstand the stresses associated with such arid conditions, it is nonetheless vulnerable to climate variability (Du Toit et al., 2018; Schmiedel & Oldeland, 2018a). Such stresses could become even more acute in future with predicted climate change impacts that would result in hotter and drier prevailing conditions and more frequent drought events (Midgley & Thuiller, 2007; Davis et al., 2016; Scholes, 2020).

In addition to climate drivers, the Succulent Karoo has historically also been subject to extensive livestock grazing (Hoffman et al., 2018). Negative impacts on species and life forms due to intensive grazing in the Karoo have been reported in various studies (Anderson & Hoffman, 2007; Haarmeyer et al., 2010; Rutherford & Powrie, 2010; Hanke et al., 2014; Van Rooyen et al. 2015; Nenzhelele et al., 2018; Schmiedel & Oldeland, 2018a, 2018b; Van der Merwe et al., 2018; Van der Merwe & Milton, 2019). Arid region ecosystems are also slow to recover from overgrazing, with rangeland improvement not readily occurring after livestock reduction (Wiegand & Milton, 1996; Todd & Hoffman, 1999; Cody, 2000; Kraaij & Milton, 2006; Lawley et al, 2013; Schmiedel & Oldeland, 2018b; Van Rooyen et al. 2015).

The mechanics of vegetation dynamics in arid rangelands are complex with divergent views on interactions and responses of vegetation to environmental drivers and grazing pressure. Equilibrium theory holds that close coupling exists between vegetation and grazing pressure via an internally driven system (Dijkstershuis 1949; DeAngelis & Waterhouse 1987), resulting in continuous but reversible progression within a single state according to the classic Clementsian theory of succession. Non-equilibrium theory on the other hand downplays the significance of these internal control mechanisms, placing more emphasis on climatic factors as primary driver of vegetation dynamics within the context of more stochastic climate environments (Ellis & Swift, 1988; Briske et al. 2003). Within such stochastic environments a coefficient of variation of 33% or more in annual rainfall is considered the threshold for non-equilibrium vegetation dynamics to prevail (Ellis & Swift, 1988; Wehrden et al., 2012). In practice none of the two theories holds sway exclusively, with arid rangeland dynamics rather displaying an interwoven combination of both equilibrium and non-equilibrium elements (Briske et al. 2003; Derry & Boone, 2010; Van Rooyen et al. 2015, 2018). It has been acknowledged that the two concepts require integration (Derry & Boone, 2010; Miehe et al. 2010).

There is currently a limited number of continuous *in situ* long-term vegetation monitoring studies in the Succulent Karoo to elucidate the long-term vegetation dynamics of the Biome (Jürgens et al., 1999; Schmiedel et al. 2012; Schmiedel & Oldeland, 2018a, 2018b; Van der Merwe & Milton, 2019; Van Rooyen et al., 2015, 2018) and even fewer on drought specific impacts (Milton et al. 2022, a diachronic study comparing the 2018 and 2020 drought years; Schmiedel & Oldeland 2018a, a continuous 17 year study up to 2017, which included the initial phase of the same drought reported in the current study).

The current study was conducted from 2010 to 2022 through continuous annual vegetation surveys in the Goegap Nature Reserve, South Africa. The region experienced a prolonged drought from 2015 to 2022. The study area was used for livestock grazing prior to its incorporation into the conservation area in 2009 and had been subjected to increasing grazing pressure from wildlife as a conservation area, up to the onset of drought conditions in 2015. In 2016, shortly after the onset of the drought, large herbivore numbers were reduced significantly in response to rangeland deterioration. The current study aims to describe the changes in rangeland condition, vegetation composition and diversity parameters over the period in relation to rainfall and grazing pressure. Vegetation composition was analysed in the context of prevailing theories of arid rangeland dynamics, *sensu* equilibrium/non-equilibrium concepts. By focussing on the perennial plant component of the vegetation assemblage the study can provide insights on the extent to which the most stable component of the rangeland has been affected by severe climatic conditions and grazing.

Study area

Goegap Nature Reserve is situated approximately 15 km east of the town of Springbok in Namaqualand, in the northwestern region of the Republic of South Africa (Figure 1). The reserve expanded gradually since its establishment in 1966 and now covers an area of 36 960 ha. The two farms Ratelkraal and Ratelkraal Restant, hereafter referred to as Ratelkraal, were added to the reserve in 2009. Ratelkraal was previously used for livestock farming. After inclusion into the reserve wildlife were allowed to gradually enter the property from the original Goegap Nature Reserve from 2010 via gates that were left open and selected gaps created in the fence separating the two areas. The mountainous terrain between Ratelkraal and the original Goegap Nature Reserve section is not readily traversed by the large herbivore species that are present. The wildlife that utilise Ratelkraal are not exclusively resident to it and are not separated from other reserve areas, since the reserve is managed as an open conservation area. The total reserve wildlife stocking density has declined from the first half of the monitoring period through active wildlife reductions and reserve expansions that have occurred in the conservation area (Figure 2).

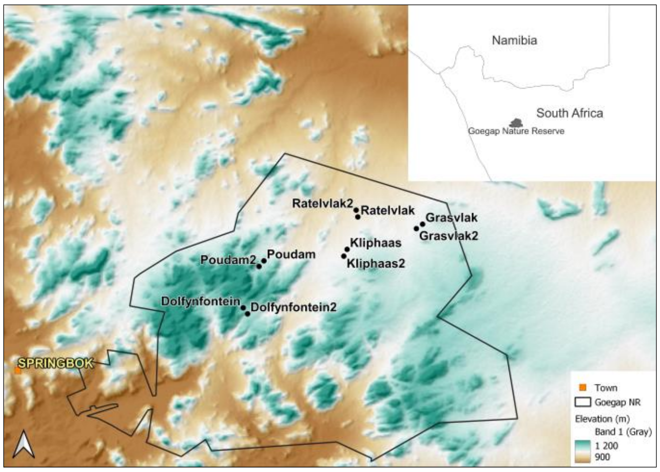


Fig. 1. Location of the Goegap Nature Reserve and the five long-term monitoring transects of 500 m each located on the Ratelkraal section of the reserve. For each transect the start and end point is indicated for example, Poudam = start point; Poudam2 = end point. {SINGLE COLUMN FITTING}

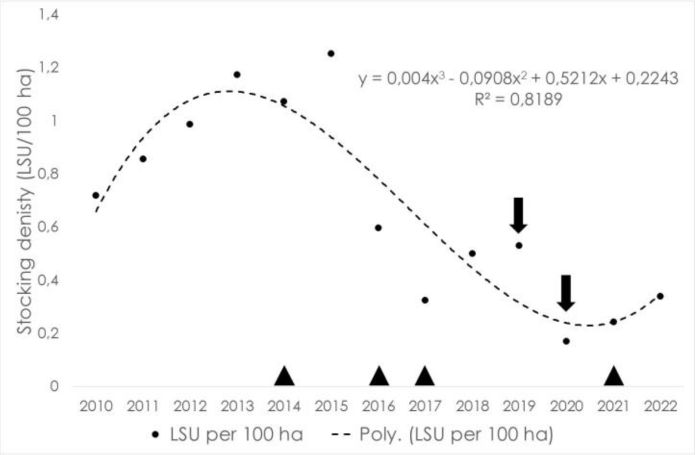


Fig. 2. Change in stocking density (Large Stock Units per 100 hectares) over the entire Goegap Nature Reserve over the monitoring period. Arrows indicate periods of reserve expansion and triangles periods of active wildlife reductions. {SINGLE COLUMN FITTING}

The reserve is characterised by typical Namaqualand landscapes in the west where gneiss/granite hills belonging to the Namaqua-Natal Metamorphic Province (Cornell et al. 2006) dominate, interspersed with valleys and sandy plains covered with early Tertiary to more recent deposits of sand. The vegetation on the hilly to mountainous terrain is classified as the Namaqualand Klipkoppe Shrubland, and the vegetation in the valleys and plains as Namaqualand Blomveld (Mucina & Rutherford 2006). In the east the landscape flattens out to large expanses of deep, sandy plains interspersed with areas of shallow soils or gravel beds as well as isolated rocky outcrops. These sandy plains are classified as Bushmanland Arid Grassland (Mucina & Rutherford 2006). Perennial plants are mainly summer-deciduous or evergreen, succulent dwarf shrubs, but in the Bushmanland Arid Grassland stands of perennial grass species are an additional floristic feature. The region is known for mass emergence of winter-growing annuals that result in scenic floral displays (Cowling et al., 1999). The emergence, successful flowering and species composition of the annuals is however dependent on rainfall quantity and rainfall seasonality, which is highly variable between years (Van Rooyen et al. 1991).

The study area has a climate of low and unpredictable rainfall. Although the eastern section of the reserve is classified as Bushmanland Arid Grassland, which is typified as being summer rainfall dominated, the study area lies on the western margin of this expansive vegetation unit. Winter rainfall is therefore still dominant on the Ratelkraal study area, but with a rain shadow from the eastern mountainous terrain reducing rainfall in comparison with the western areas of the reserve. The mean annual rainfall recorded on Ratelkraal as measured from 1 September to 30 August for the period 1995 – 2022 is 116 mm (Figure 3), with a Coefficient of Variation of 57.9%. This period is indicated because annual surveys were conducted in September. For the annual cycle of 1 January to 31 December mean rainfall is 115 mm per year. In comparison, the long-term mean annual rainfall for western Goegap Nature Reserve is 146 mm (Coefficient of Variation of 39.6%).

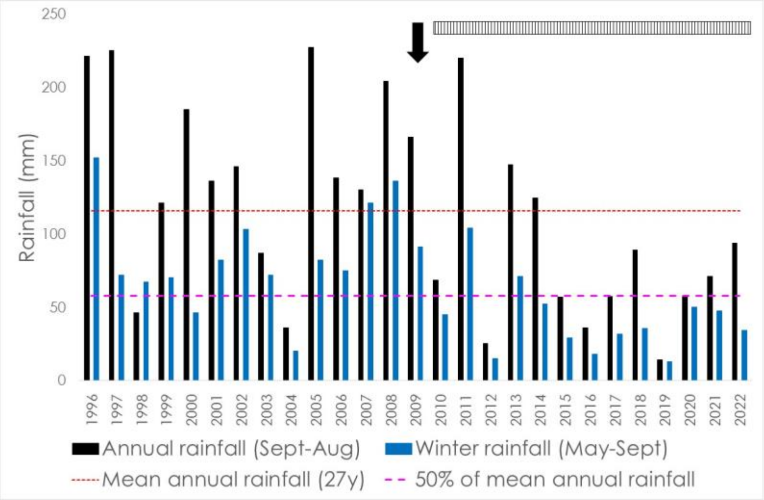


Fig. 3. Rainfall data for the monitoring period at Ratelkraal indicating annual (Sept – Aug) and winter (May – Sept) rainfall. Annual rainfall of below 50% of mean annual rainfall is regarded as severe drought. The arrow indicates the year of inclusion of Ratelkraal into the conservation area and the bar the period over which this study was conducted. {SINGLE COLUMN FITTING}

Methods

Field survey

In 2010 an array of monitoring sites were established on Ratelkraal, with the five sites of this study being monitored annually (Figure 1). The individual 500 m monitoring transects were permanently marked with metal rods at each 100 m (Figure 4).

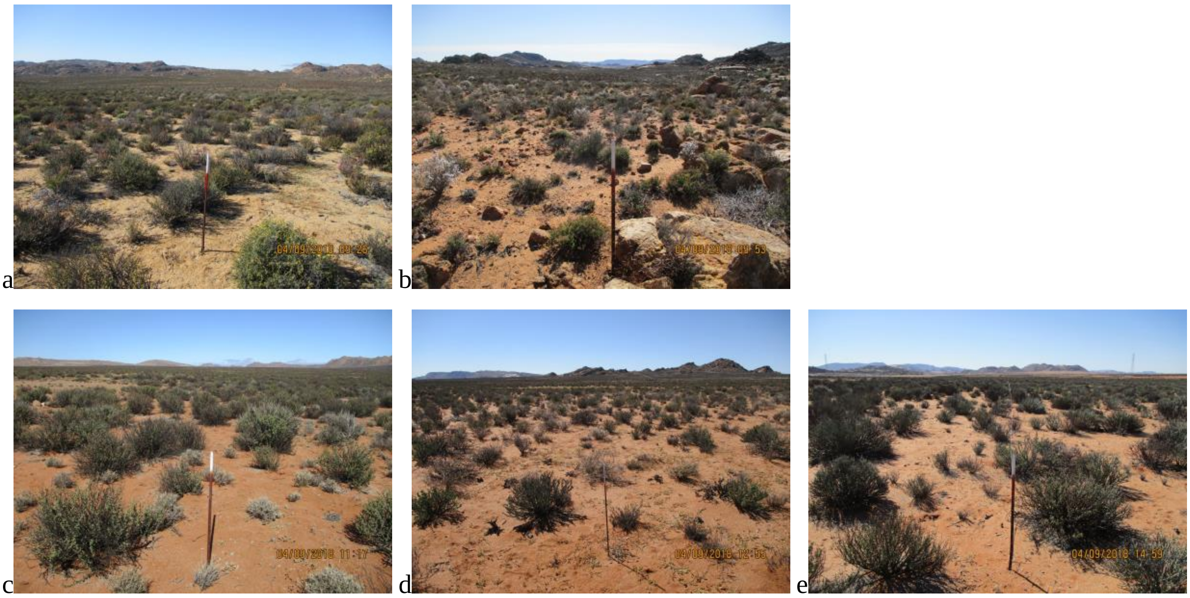


Fig. 4. Photographs of the starting points of the five monitoring transects: (a) Dolfynfontein and (b) Poudam, the two hilly habitats; (c) Kliphaas, (b) Grasvlak and (d) Ratelvlak, the three sandy plains habitats. Photographs by C. Geldenhuys. {2 COLUMN FITTING}

The sites can be grouped into two sets based on environmental features: the two hilly, western sites, Dolfynfontein (plateau) and Poudam (valley), and the three eastern plains sites Kliphaas, Grasvlak and Ratelvlak (Figure 1). All the sites are underlain by granites and gneisses of the Namaqua-Natal Metamorphic Province, but with the eastern plains overlain by early to recent tertiary sands. The eastern plains are classified as Ae80 Land Type with red, high base status soils, slopes of 1-12% and 5-10% cover of rock, stones and boulders (Land Types Survey Staff 1987). The western hills are classified as Land Type Ib127 with generally steeper slopes of up to 90% and 60-80% cover of rock, stones and boulders (Land Types Survey Staff 1987). Hutton soil forms dominate all sites. At the plant association level the three plains monitoring sites are classified as *Ruschia robusta* – *Stipagrostis brevifolia* – *Osteospermum sinuatum* – *Othonna arbuscula* Plains Dwarf Shrubland, whereas the hilly Dolfynfontein and Poudam sites are classified as *Ruschia brevibracteata* – *Ruschia robusta* – *Eriocephalus microphyllus* Valley Dwarf Shrubland (Van Rooyen & Van Rooyen, unpublished report). At the Dolfynfontein monitoring site there is also an intrusion of *Roepera foetida* – *Searsia undulata* – *Callobota sericea* Mountain Dwarf Shrubland.

The eastern plains habitat is more suitable for resident wildlife such as gemsbok (*Oryx gazella*) and springbok (*Antidorcas marsupialis*), although Hartmann's mountain zebra (*Equus zebra hartmannae*) utilise both hills and plains habitats. A summary of the environmental context of the five monitoring sites is provided in Table 1.

Table 1 Environmental context of the five monitoring sites on Goegap Nature Reserve {1.5 COLUMN FITTING}

Site	Altitude	Topography and terrain	Primary vegetation structure	Recent land use history
Dolfynfontein	1130 m	Plateau among rocky hills, slightly undulating, intermittent base rock outcrops, shallow granitic soils	An assemblage of succulent and non-succulent shrubs with possible understory of dwarf shrubs and herbs. A sheltered habitat that can support high annual cover and density, under and between shrubs	In the last years prior to inclusion (pre-2009) farmed at low intensity. Located in the vicinity of a fence gate that provided wildlife access to Ratelkraal after inclusion, but the terrain is not readily accessible to plains game. Would have been remote during the farming era
Poudam	1090 m	Valley among rocky hills, slightly undulating, shallow to gravelly granitic soils, adjacent to a drainage line	In comparison with Dolfynfontein, a lower and sparser assemblage of succulent and non-succulent shrubs and dwarf shrubs. Presence of annuals rarely prolific	In the last years prior to inclusion (pre-2009) farmed at low intensity, but only 1 km from an old watering point and 2 km from homestead
Kliphaas	1056 m	Sandy plain, flat topography, deep tertiary deposits	Mostly succulent shrubland interspersed with perennial grass. Round circles denuded of perennial vegetation called "heuweltjies" are prominent	In the last years prior to inclusion (pre-2009) farmed at low intensity, but central to grazing activity by wildlife as well as livestock historically
Grasvlak	1061 m	Sandy plain, flat topography, deep tertiary deposits	Assemblage of succulent and non-succulent shrubs, dwarf shrubs and perennial grasses	In the last years prior to inclusion (Pre-2009) farmed at low intensity, but important to grazing activity by wildlife as well as livestock historically
Ratelvlak	1039 m	Sandy plain, flat topography, intermittently compacted sedimentary ridges (dorbank), otherwise deep tertiary deposits	Succulent shrubs and dwarf shrubs dominant with secondary presence of perennial grasses and non-succulent shrubs and dwarf shrubs	Heavily grazed by livestock prior to inclusion (pre-2009) by a different land owner to the other four sites. More degraded from overgrazing than the other two plains sites

Surveys were conducted annually in spring (August to October), following the main winter rainfall season. Rainfall data for Ratelkraal was obtained from a manual rainfall gauge positioned next to the Kliphaas site for the period 1995 – 2022. The point intercept method (Roux 1963), was used with 500 points per survey to determine the species composition and vegetation cover at each line transect. The following data were recorded at each 1 m interval:

- first strike (foliar or canopy) = plant species first struck by the rod or within its canopy spread;
- second strike (foliar or canopy) = plant species growing beneath the first plant species that was struck by the rod or within its canopy spread.

Data analysis

The following values were calculated annually for each line transect:

- vegetation cover = number of first strikes expressed as a percentage of the total number of possible strikes (500);
- frequency per species = sum of first and second strikes;

- perennial plant species richness (S) = total number of perennial species recorded per transect;
- Shannon-Wiener index of diversity (H') for the perennial plants was computed using the equation (Krebs 1999):

  $$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

  Where S = number of species

  p_i = cover of species i expressed as proportion of total cover;

  ln (p_i) = the natural logarithm of the proportional cover of species i.
- species evenness for the perennial plants was computed using the equation:

  $$E = H'/\ln(\text{Richness})$$
- Simpson's index of diversity for the perennial plants was computed using the equation:

  $$D = -\sum_{i=1} p_i p_i$$

  Where p_i = cover of species i expressed as proportion of total cover;

To account for changes in the life form composition, each species was assigned to a life form category according to the Raunkiaer Plant Life Form classification of Mueller-Dombois and Ellenberg (1974). The frequency of abundance per life form (nanophanerophytes, stem succulent chamaephytes, leaf succulent chamaephytes; frutescent chamaephytes, suffrutescent chamaephytes, hemicryptophytes, geophytes and therophytes) was calculated as the sum of first and second strikes. Leaf succulent chamaephytes and stem succulent chamaephytes were combined to calculate succulent life form abundance. Frutescent chamaephytes, suffrutescent chamaephytes and caespitose nanophanerophytes were combined to calculate non-succulent life form abundance. In the Raunkiaer Plant Life Form scheme succulent chamaephytes are identified as plants where the perennial, lignified shoots remain within 500 mm of the ground as is found in the South African deserts (*sensu* Succulent Karoo) or that grow taller than 500 mm but die back periodically to that height. In the Succulent Karoo such succulent shrubs often exceed 500 mm, with perennial shoots commonly carried up to 1 m height. The chamaephyte designation is nonetheless consistently applied in this study since the nearest alternative classification of succulent phanerophyte does not adequately describe the characteristics of these life forms.

Principal Coordinates Analysis (PCoA) ordinations were conducted in the PC-Ord version 6 (McCune & Grace, 2002; McCune & Mefford, 2011) to illustrate the trajectories of the perennial component at all five sites. Ordinations were also used to group the floristic data of the monitoring sites. For the ordinations, the cover values were standardised using a natural logarithmic ($\log_e$) standardisation. The Bray-Curtis measure was applied for the ordinations.

To examine the effects of annual rainfall (September – August, annual rainfall preceding the survey) and winter rainfall (May – September) as well as stocking density of large herbivores gemsbok, springbok, Hartmann's mountain zebra and ostrich on the floristic composition, a second matrix was compiled containing various rainfall parameters and stocking densities. Pearson correlations between the PCoA axes and the variables in the second matrix were calculated by means of PC-Ord.

To determine whether the changes occurring in the vegetation were positive or negative the range condition was assessed using the Grazing Index Method (GIM) of Du Toit (2000, 2003). This method is a refinement of the method originally proposed for Karoo veld by Vorster (1982). The method uses the ecological status of the plant species as determined by their grazing index values (Du Toit 2000, 2003). To calculate the grazing capacity the range condition score was compared with a benchmark with a known grazing capacity (Du Toit 2003).

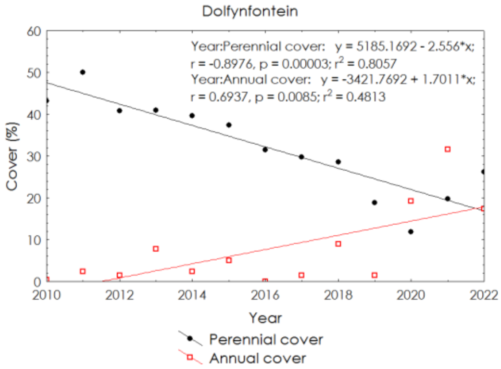
Results

Rainfall

Mean annual rainfall (January – December) on Ratelkraal over the 28 year rainfall data period was 115 mm with a coefficient of variation of 50.4%. Winter rainfall (May – September) contributed 31 – 100% (mean of 59%) of the total annual rainfall. Over the study period rainfall for ten of the thirteen years was below the long term mean, and for six of the thirteen years rainfall was less than 50% of the long term mean (extremely low).

Canopy cover of annual and perennial species

In the two mountainous habitats a significant linear downward trend in perennial plant cover was observed over the monitoring period (Figure 5) (Dolfynfontein R^2=0.8057, p=0.00003; Poudam R^2=0.8610, p=0.00000) but a significant upward trend in annual plant cover (Dolfynfontein R^2=0.4813, p=0.0085; Poudam R^2=0.3675, p=0.0281). In the three plains habitats a similar significant downward trend was observed in perennial plant cover (Kliphaas R^2=0.7732, p=0.00007; Grasvlak R^2=0.7690, p=0.00008; Ratelvlak R^2=0.7555, p=0.00001). There was however no significant trend in annual vegetation cover over the monitoring period in any of the plains habitats (Figure 5). Annual vegetation cover reacted to inter-annual variation in rainfall (Supplementary Material D).



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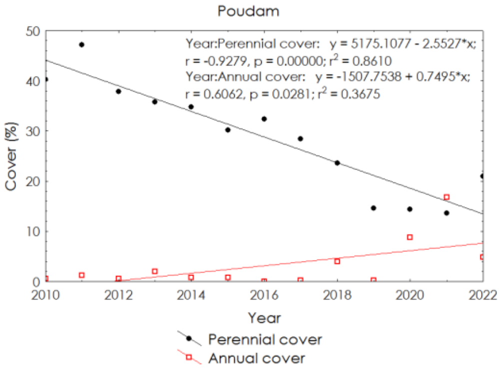

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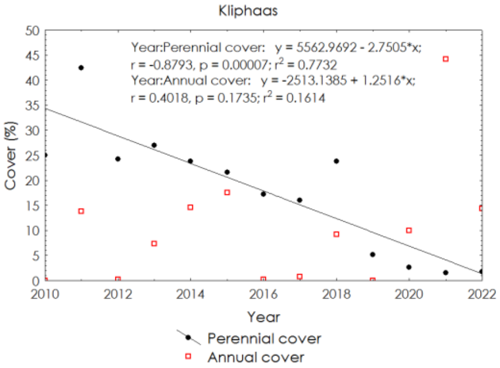

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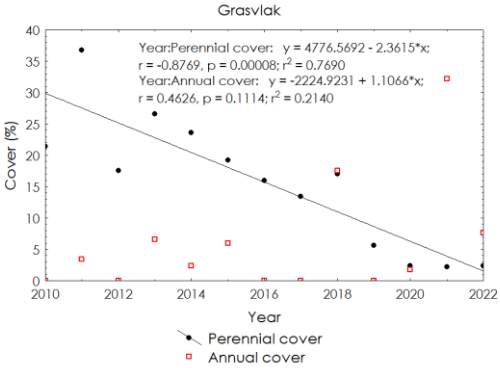

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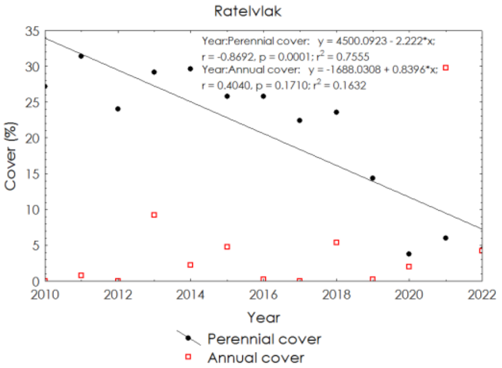

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Fig. 5. Changes in perennial and annual canopy cover over the monitoring period at the two mountainous sites (a) Dolfynfontein and (b) Poudam, and the three plains sites (c) Kliphaas, (d) Grasvlak and (e) Ratelvlak. Only significant relationships are connected by lines. {SINGLE COLUMN FITTING PER GRAPH OR DOUBLE COLUMN FITTING AS A GROUP}

Perennial plant species richness and perennial plant diversity

Perennial plant species richness was consistently higher throughout the study period in monitoring sites located in the mountainous habitat in comparison to monitoring sites in the plains habitat (Supplementary Material A). Dolfynfontein had the highest species richness (mean=26.6), followed by Poudam (mean=22.6), with the plains sites Ratelvlak (mean = 11.3), Grasvlak (mean=8.1) and Kliphaas (mean=6.9) distinctly lower.

Between monitoring sites species diversity variables changed inconsistently over time in both direction and significance (Supplementary Material B). In the Dolfynfontein mountainous habitat site species richness declined over time (R^2=0.5998; p=0.0019) whereas species evenness increased (R^2=0.6675; p=0.0005). Since the Shannon-Wiener index of diversity accounts for both species richness and plant cover, this index did not show any significant trend over time due to the opposing trends of species richness and species evenness. Simpson's index of diversity did however increase significantly over time (R^2=0.6093; p=0.0016). Poudam, as the other mountainous habitat site, did not show any significant trend over time for species richness, species evenness, Shannon-Wiener index of diversity or Simpson's index of diversity.

At the Kliphaas plains monitoring site the diversity trends were similar to the mountainous Dolfynfontein monitoring site: Species richness declined (R^2=0.6615; p=0.0007) and species evenness increased (R^2=0.6716; p=0.0006), but with neither Shannon-Wiener index of diversity nor Simpson's index of diversity yielding any significant trend. In the Grasvlak plains habitat, species richness declined significantly ((R^2=0.6419; p=0.0010), but not at Ratelvlak. At Ratelvlak species evenness did increase significantly (R^2= 0.5550; p=0.0035) and at Grasvlak it did not. At the Ratelvlak monitoring site both Shannon-Wiener index of diversity (R^2=0.3320; p=0.0431) and Simpson's index of diversity (R^2=0.4674; p=0.0100) increased significantly, due to the strong increase in species evenness. Conversely in the Grasvlak habitat both Shannon-Wiener index of diversity (R^2=0.4523; p=0.0118) and Simpson's index of diversity (R^2=0.3914; p=0.0222) declined significantly due to a strong decrease in species richness.

Correlations between diversity variables are available in Supplementary Material C.

Life form composition

Both the non-succulent life form group (comprising the combination of frutescent chamaephytes, suffrutescent chamaephytes and caespitose nanophanerophytes) and the succulent life form group (comprising the combination of leaf succulent chamaephytes and stem succulent chamaephytes) declined significantly over the monitoring period across all sites, except for the non-succulent life form group in the Ratelvlak site (Figure 6). The non-succulent shrub life form group at the Ratelvlak and Kliphaas sites had extremely low mean abundances of 1.77% and 0.67% respectively over the monitoring period, which hampered meaningful deductions of change in this life form group for these two sites.

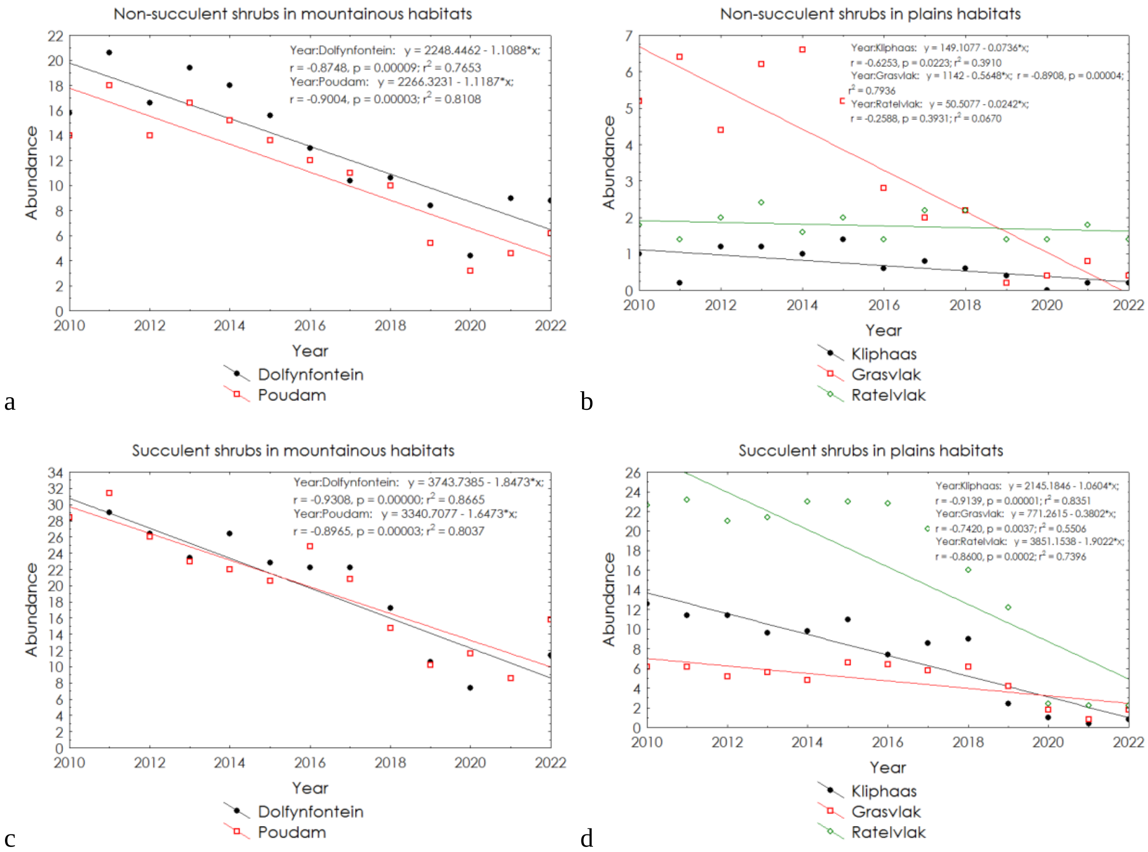

Fig. 6. Changes in non-succulent chamaephyte (shrub) abundance at (a) the two mountainous sites Dolfynfontein and Poudam and (b) at the three plains sites Kliphaas, Grasvlak and Ratelvlak. Changes in succulent chamaephyte (shrub) abundance at (c) the two mountainous sites Dolfynfontein and Poudam and (d) at the three plains sites Kliphaas, Grasvlak and Ratelvlak. Leaf succulent chamaephytes and stem succulent chamaephytes were combined to calculate succulent shrub abundance. Frutescent chamaephytes, suffrutescent chamaephytes and caespitose nanophanerophytes were combined to calculate non-succulent shrub abundance. Only significant relationships are connected by lines. {SINGLE COLUMN FITTING PER GRAPH OR DOUBLE COLUMN FITTING AS A GROUP}

Range condition

The range condition score for all five monitoring sites declined significantly over the monitoring period (Dolfynfontein R^2=0.8600, p=0.00001; Poudam R^2=0.8645, p=0.00000; Kliphaas R^2=0.8233, p=0.00002; Grasvlak R^2=0.8356; p=0.00001, Ratelvlak R^2=0.7966; p=0.00004), (Figure 7). The initial range condition score for the mountainous habitats was higher (Dolfynfontein 111.4 at the start and maximum of 127.0; Poudam 100.0 at start and maximum of 115.6) than the plains habitats (Kliphaas 76.7 at start and maximum of 117.3; Grasvlak 67.2 at start and maximum of 99.7; Ratelvlak 70.8 at start and maximum of 73.7). The higher range condition score of the mountainous habitats was maintained over the monitoring period but with the important element that at the end of the monitoring period (2022) the range condition in the plains habitats was a much lower percentage of the high recorded at the start of the monitoring period than in the mountainous habitats (data not shown, Dolfynfontein=45.2% of high; Poudam=42.6% of high; Kliphaas=3.6% of high; Grasvlak=6.7% of high; Ratelvlak=13% of high).

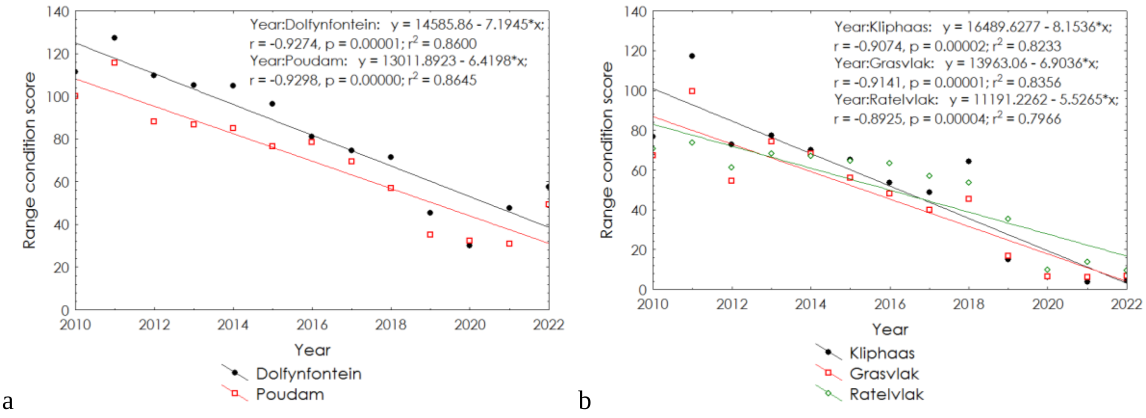

Fig. 7. Change in Range Condition Score at (a) the two mountainous sites Dolfynfontein and Poudam and (b) at the three plains sites Kliphaas, Grasvlak and Ratelvlak. {SINGLE COLUMN FITTING}

Range condition score correlated significantly with perennial cover in all habitats (Supplementary Material C). In four of five monitoring sites range condition also correlated significantly with perennial species richness, species evenness, and Simpson’s index of diversity. Range condition did not consistently correlate with Shannon-Wiener index of diversity as only two of the five monitoring sites had significant correlations.

Floristic composition

The PCoA ordination of perennials for all monitoring sites showed a clear separation of the two mountainous sites from the three plains sites (Figure 8). Within the two major habitat groupings there was also separation between the individual monitoring sites. In all sites a directional change in the floristic composition was observed. The extent of the directional change was much larger in the three plains sites than in the two mountainous sites. The individual monitoring sites within the two major habitat groups had similar directions and extent of change, *viz.* the two mountainous sites moved slightly and in a similar direction, whereas the three plains sites moved noticeably and in a similar direction.

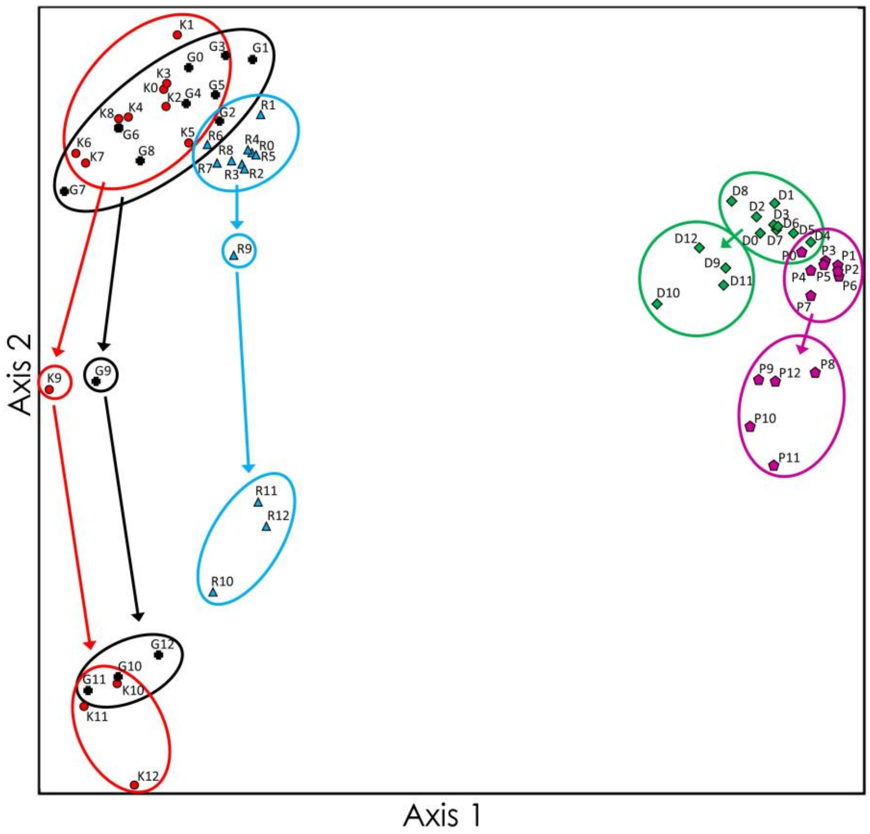

Fig. 8. Principal Coordinates Analysis scatter diagram of perennial species' floristic data for all five monitoring sites. Letters indicate the monitoring sites: D = Dolfynfontein (green), P = Poudam (pink), G = Grasvlak (black), K = Kliphaas (red), R = Ratelvlak (blue). Numbers indicate monitoring years, e.g. 1 = year 1, 2 = year 2. The three monitoring sites on the left in the ordination are plains habitat sites and the two monitoring sites on the right are mountainous habitat sites. {DOUBLE COLUMN FITTING}

The PCoA ordinations of individual monitoring sites showed more detail of the floristic change over the monitoring period (Figure 9). At Dolfynfontein (Figure 9a) and Poudam (Figure 9b) 2017 – 2020 was a phase of distinct change from the preceding quasi-stable period. The directional change in both sites started to recurve back somewhat towards the origin at the end of the monitoring period in 2022. At the three plains sites Grasvlak (Figure 9c), Kliphaas (Figure 9d) and Ratelvlak (Figure 9e) change manifested from 2018 or 2019 to 2020. The direction of change in the three plains habitats continued on a trajectory away from the original composition to the end of the monitoring period.

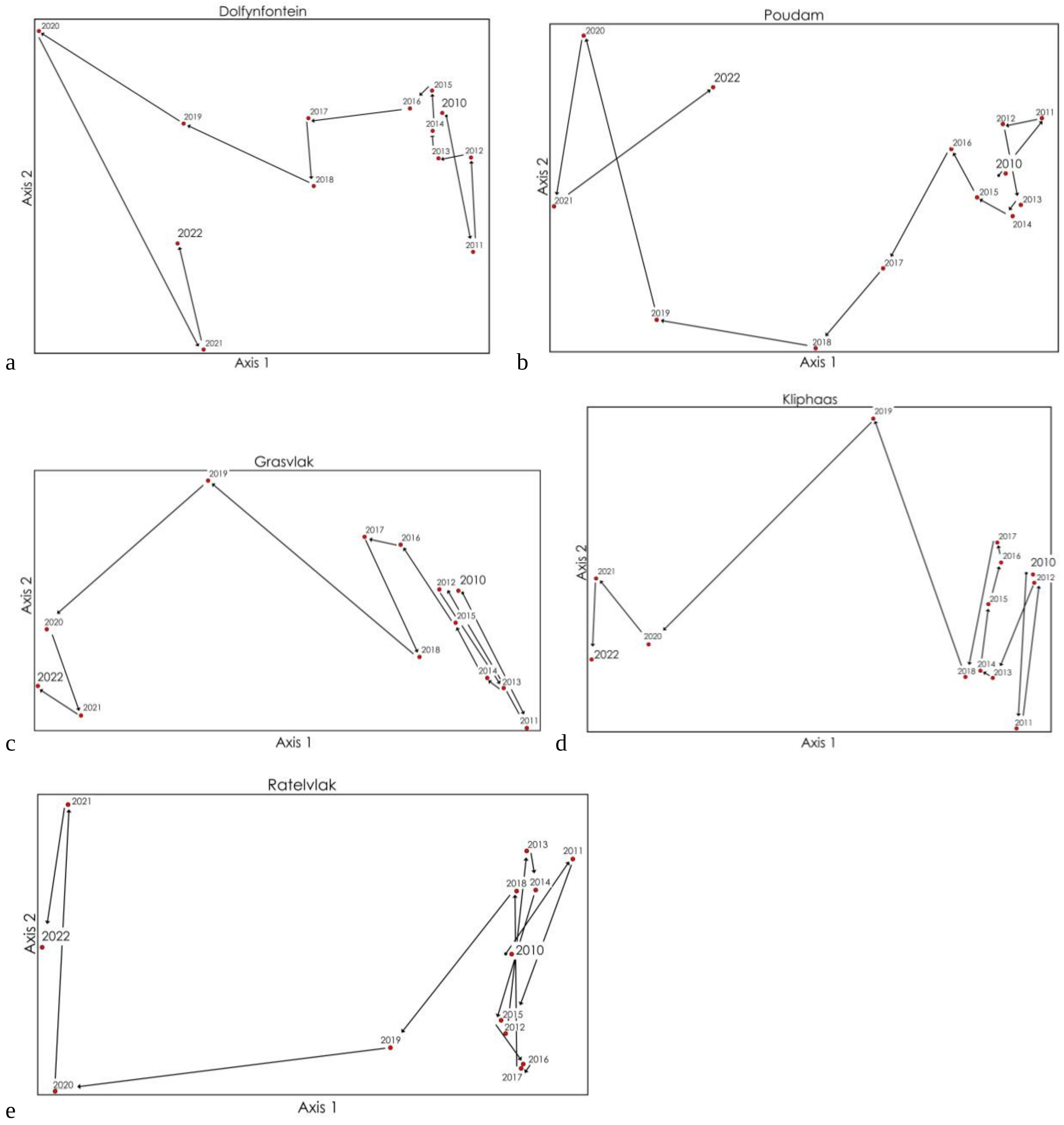

Fig. 9. Principal Coordinates Analysis scatter diagram of perennial species floristic data for the five monitoring sites (a) Dolfynfontein, (b) Poudam, (c) Grasvlak, (d) Kliphaas and (e) Ratelvlak. Numbers indicate monitoring years. {SINGLE COLUMN FITTING PER GRAPH OR DOUBLE COLUMN FITTING AS A GROUP}

Large herbivore population sizes

The indirect Pearson's correlation of rainfall and large herbivore populations with the PCoA ordination axes provided more insight into floristic composition changes (Table 2). In the plains sites large herbivore population size was associated with Axis 1 and rainfall (annual and winter rainfall) was associated with Axis 2.

At the mountainous monitoring sites large herbivore population size was associated with Axis 1 but there was no strong relationship with either rainfall parameter. The Hartmann's mountain zebra population size relationship with Axis 1 was in an opposing direction (towards the latter years of the monitoring period) to the population sizes of gemsbok, springbok and ostrich (which was towards the initial years of the monitoring period). Population sizes of gemsbok, springbok and ostrich were greatly reduced during the first half of the monitoring period through active interventions (Figure 2).

Table 2 Indirect Pearson's correlation of rainfall and large herbivore population sizes with the first two axes of the Principal Coordinates Analysis (PCoA) ordination for the five monitoring sites floristic data. Only R^2 values of more than 0.2 are indicated {DOUBLE COLUMN FITTING}

Pearson's correlation (R^2)	Dolfynfontein		Poudam		Kliphaas		Grasvlak		Ratelvlak	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Annual rainfall (Sept-Aug)						0,641		0,589		0,484
Winter rainfall (May-Sept)						0,520		0,536		0,396
Gemsbok	0,628		0,619		0,437		0,590		0,432	
Hartmann's mountain zebra	0,388		0,445		0,538		0,487		0,455	
Springbok	0,619		0,611		0,726		0,685		0,764	
Ostrich	0,470		0,488				0,300			

Discussion

In the present study the primary environmental feature was the low rainfall recorded over the monitoring period. For ten of the thirteen years annual rainfall was well below the norm and this included a continuous eight year drought period over the latter years of the study. Even though high inter-annual rainfall variability is a feature of the Namaqualand region of the arid Succulent Karoo, this extended drought period is an extreme event and extended drought is a rare occurrence (Desmet & Cowling, 1999). The study area has a 200 year prior history of livestock farming as well as natural wildlife utilisation prior to human settlement (Milton & Dean, 2021; Hoffman et al., 2018). Dissecting these complex histories of rainfall and grazing disturbance together with social components remains complex and difficult (Milton & Dean, 2021; Scholes, 2020). It is nonetheless possible to describe some medium term dynamics for these landscape factors through this study.

Plant cover, perennial plant diversity and perennial plant life forms

Annual plant cover in arid regions is known to be highly variable and largely dependent on suitable rainfall (Van Rooyen et al. 1991; Schmiedel & Oldeland, 2018a; Van Rooyen et al., 2018). A similar pattern is also evident over this drought period with ephemeral plants responding to minimal moisture availability even during an overall drought period. Over the monitoring period as a whole however there is no discernible linear trend in annual plant cover, confirming inter-annual rainfall as a strong determining factor. The one mountainous habitat that showed a positive trend over the study period must be seen in the context of the preceding drought years and an outsized response of annual vegetation to moisture availability after an exceptionally dry preceding year. The annual vegetation component provides a valuable, however not a reliable source of fodder for rangelands or provide any buffering facility against environmental stresses (Nenzhelele et al., 2018).

At all monitoring sites perennial plant cover declined, which is of great concern in the management of ecological condition and land productivity. In comparison with plains habitats, the mountainous habitats had higher perennial plant cover at the onset of the study and also ended the monitoring period with higher plant cover. In the plains habitats perennial plant cover declined catastrophically with cover approaching zero at the extremes in some sites. In contrast to plains habitats where these declines led to the disappearance of dominant perennial shrubs or grasses such as *Osteospermum sinuatum, Ruschia robusta* and *Stipagrostis brevifolia*, in mountainous habitats perennial shrubs were able to persist. The drought did not impact differentially between succulent and non-succulent life form abundance in any of the habitats, with both groups showing steep declines. This in contrast to experimental predictions that non-succulent shrubs could be more drought tolerant than succulent shrubs (Midgley & Thuiller, 2007). Of note though is that the dominant succulent shrub *Ruschia robusta* experienced a rapid decline in the plains habitats from 2019 unlike the gradual decline of the species in the mountains, pointing towards a tipping point having been reached. In the mountainous habitats a degree of recovery in the life form groups were visible at the end of the study period but no sign of any recovery had manifested in plains habitats. These trends together with the shallower slope of decline in mountainous habitats indicates the higher resilience of mountainous habitats when compared to plains habitats in the face of an extreme drought event. The higher susceptibility of lower lying areas to grazing pressure in comparison with uplands is consistent with expectations and other reports for the region (Todd & Hoffman, 1999; Anderson & Hoffman, 2007; Van Rooyen et al., 2015, 2018). In a tri-annual study (1996, 2006, 2016) of vegetation responses in the Namaqualand Blomveld vegetation unit 80 km south of our study, no observable changes were found in the cover of succulent shrubs, woody shrubs or perennial grasses over that period, noting that it terminated at the start of the drought and did not include an extended drought period (Nenzhelele et al., 2018). In another continuous study from 2002 – 2017 in Namaqualand Heuweltjieveld 80 km southwest of our study, a general oscillation in perennial plant cover was observed and a gradual increase in species richness over time after a decrease in grazing pressure (Schmiedel & Oldeland, 2018a). The trends in species richness and perennial plant cover reversed however in the last year of that study in 2017 after a dry spell in that year. As previously stated 2015 – 2017 represented the start of the regional drought.

In the two sites of the current study where opposing trends manifested of decreasing species richness and increasing species evenness (a function of relative plant cover) a deleterious effect on species diversity occurred (which considers both species richness and cover variables). This resulted in mostly an absence of directional trends in diversity indices over time to the drought event. On one site where species richness showed no trend but species evenness increased, the two diversity indices also increased. The single site in which species richness decreased without a significant trend in species evenness, resulted in the two diversity indices declining. This array of potential response in a single study to various diversity parameters shows that the context must be understood to gauge responses. A decline in species richness may be offset by an increase in species evenness, resulting in stable species diversity (with Shannon-Wiener index of diversity and Simpson's index of diversity as examples). Stated differently, stable species diversity could mask a decline in species richness.

Range condition and large herbivore populations

During the initial stages of the study rangeland was subjected to grazing pressure from wildlife. The negative coupling between grazing pressure and rangeland condition has been firmly established in arid rangelands (Todd & Hoffman, 1999; Anderson & Hoffman, 2007; Du Toit et al., 2018; Haarmeyer et al., 2010; Hanke et al., 2014; Rutherford & Powrie, 2010; Schmiedel & Oldeland, 2018b; Van der Merwe & Milton, 2019; Van Rooyen et al., 2015). The deterioration in rangeland condition in monitored habitats had started before the onset of the main drought period from 2015. The deterioration continued to progress despite regular efforts to reduce grazing pressure through wildlife removal activities, with rainfall subsequently becoming the primary driver of rangeland condition. In the plains habitats rangeland condition deteriorated more than in mountainous habitats without evidence of stabilising or reversing by the end of the study period. In fact, rangeland condition of some monitoring sites had approached an absolute minimum value. In contrast mountainous habitats had reached a period of stabilisation or had begun to slightly improve in the latter part of the monitoring period, even with a modest improvement in rainfall. The superior ability of mountainous habitats to absorb disturbance and potential to recover from severe environmental impact is therefore evident. The inertia behind this recovery is however uncertain since arid rangeland improvement (after grazing pressure reduction) is extremely slow (Wiegand & Milton, 1996; Todd & Hoffman, 1999; Van Rooyen et al., 2015; Schmiedel & Oldeland, 2018a). Plains are the preferred habitat of livestock and wildlife and this grazing pressure has been exerted on the plains vegetation over many years, resulting in depressed resilience and recovery potential from the onset. These legacy effects are evident from long-term vegetation studies (Van Rooyen et al., 2015, 2018). Interpreting or predicting Succulent Karoo vegetation recovery from extended drought is problematic due to a lack of regional reference studies. Existing regional long-term vegetation studies are either of extended duration but diachronic or with extended intervals (Du Toit et al., 2018; Nenzhelele et al., 2018; Rahlao et al., 2008), or are continuous medium-term studies spanning a decade or two but which do not contain any extended drought periods (Jürgens et al.,1999; Schmiedel et al. 2012; Schmiedel & Oldeland, 2018a), or are short-term drought response studies (Milton et al., 2022). Continuous assessment over extended periods (>15y.) is required to understand how degradation from grazing and drought has embedded in the vegetation of arid landscapes (Miehe et al., 2010).

Floristic composition and vegetation dynamics

Floristic composition at each of the five monitoring sites remained relatively constant over the initial period of 2010 – 2015. As the drought started to take hold the mountainous habitats species composition began a gradual shift away from the existing composition from 2017 onwards. In contrast to the mountainous habitats, the plains habitats transition away from the existing composition was much more abrupt. The exceptionally dry 2019 year triggered a rapid species composition change from 2019 onwards. The difference in the magnitude of the change in species composition between mountainous and plains habitats confirms that mountainous habitats are more resilient to drought impact. This resilience is supported further by the tendency of the mountainous habitat floristic composition to return to the initial composition by the end of the monitoring period. In contrast the floristic composition of the plains habitats continued on a trajectory away from the initial composition. The higher resilience of mountainous (*sensu* upland) habitats in comparison to plains habitats in the Namaqualand region of the Succulent Karoo has been established (Anderson & Hoffman, 2007; Van Rooyen et al. 2015, 2018), although it is shown here that mountainous habitats are not exempt from drought impact. The legacy effects of differential long-term grazing pressure between uplands and lowlands on range condition also applies to floristic composition resilience.

Grazing pressure varied over the period that this study was conducted. Although grazing pressure had increased at the start of the monitoring period, this was gradually reduced through active population control. As a high conservation value species the Hartmann's mountain zebra population was never controlled and continued to increase throughout the monitoring period. Of the large herbivore species it is also the species that would most readily utilise mountainous habitats. These factors contribute to the opposing directional relationship of the species with Axis 1 of the PCoA (Table 2). The absence of a strong relationship of rainfall with the mountainous habitats ordination axes showed that rainfall had a lesser impact on the magnitude of floristic compositional change in this habitat than in the plains habitats. This points to higher resilience in mountainous habitat where, even though perennial plant mortalities were high, floristic composition remained more constant over the monitoring period. Both rainfall and grazing pressure were important drivers of species composition at the monitoring sites, but grazing was a stronger driver in the plains than in the mountains.

Equilibrium and non-equilibrium vegetation dynamics

The high coefficient of variation (>33%) in annual rainfall of our study site makes it susceptible to the prevalence of non-equilibrium vegetation dynamics (Ellis & Swift, 1988; Wehrden et al., 2012). Under such environmental conditions there is no strong coupling between internal biotic controls and grazing, with external climate factors being the primary determinants. In this study there was however a clear deterioration in rangeland condition due to high grazing pressure prior to the onset of the drought, which supports other regional observations of the negative impact that intensive grazing has on vegetation (Anderson & Hoffman, 2007; Schmiedel & Oldeland, 2018b). The initial rangeland deterioration in response to grazing pressure is consistent with the equilibrium paradigm of vegetation dynamics. This relationship is in contrast to that found in east Africa where grazing and primary production is not linked (Ellis & Swift, 1988). In the latter half of the study period the lack of rainfall became the primary driver of rangeland deterioration and vegetation composition change, which is associated with the non-equilibrium paradigm of vegetation dynamics. Non-equilibrium dynamics was also reflected in the inter-annual variation of annual vegetation cover.

Disturbance in the form of intensive grazing or severe environmental conditions can act as a catalyst for abrupt changes in vegetation, from a state-and-transition point of view (Cingolani et al. 2005; Miehe et al., 2010; Porensky et al., 2017; Van Rooyen et al., 2015). The drought in this study resulted in a clear transition from one quasi-stable state to another at all monitoring sites, with the mountainous sites change progressing slowly over a small range, but the plains sites progressing suddenly, rapidly and over a long range. This drought induced rapid change can be seen as a tipping point for the habitats in question, specifically the plains habitats.

In the context of uncertainty over the Succulent Karoo's future land capability and resilience in the face of climate change, this study revealed some alarming trends in range condition and perennial plant condition. Diversity indices do not always consistently reflect the underlying health of arid vegetation. With increasing demands being placed on land for production, whether it is agricultural or conservation-based, increased grazing pressure could amplify the effects of extreme environmental events such as drought. This is even more relevant for areas that have a long history of land use (overgrazing). The ability for perennial vegetation to recover from such an extreme drought event will only become clearer with continuous monitoring.

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Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: