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Long-term vegetation dynamics (40 yr) in the Succulent Karoo, South Africa: effects of rainfall and grazing

Margaretha W. van Rooyen, Annelise Le Roux, Conrad Geldenhuys, Noel van Rooyen, Nadine L. Broodryk & Helga van der Merwe

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van Rooyen, M.W. (corresponding author, gretel.vanrooyen@up.ac.za)[1],
Le Roux, A. (aleroux@capenature.co.za)[2]*,
Geldenhuys, C. (conradgeldenhuys@gmail.com)[3],
van Rooyen, N. (noel@ekotrust.co.za)[1],
Broodryk, N.L. (nadine.broodryk@up.ac.za)[1],
van der Merwe, H. (helga@saeon.ac.za)[4]*

[1]Department of Plant Science, University of Pretoria, Private Bag X20, Hatfield 0028, Pretoria, South Africa;
[2]CapeNature, Assegaaibosch Nature Reserve, Private Bag X5014, Stellenbosch 7599, South Africa;
[3]Northern Cape Department of Environment and Nature Conservation, Goegap Nature Reserve, Private Bag X1, Springbok 8240, South Africa;
[4]South African Environmental Observation Network (SAEON): Arid Lands Node, P.O. Box 110040, Hadison Park 8306, Kimberley, South Africa

*At the time when the surveys were conducted A. Le Roux was employed by Cape Nature Conservation and H. van der Merwe by Northern Cape Nature Conservation.

Abstract

Questions: Vegetation change in arid regions with a coefficient of rainfall exceeding 33% usually displays non-equilibrium dynamics, where abiotic factors override internal biotic controls. Irreversible changes have nonetheless also been described for arid regions. What are the contributions of internal/equilibrium vs external/non-equilibrium factors to vegetation dynamics and can degradation due to overstocking be reversed after removal of livestock?

Location: Goegap Nature Reserve, Namaqualand, South Africa.

Methods: The descending point method was conducted annually from 1974 at two transects. Vegetation change was assessed in terms of vegetation cover, species composition, life-form composition, range condition, species richness and diversity. Principal coordinates analysis was used to illustrate the trajectories in floristic data, and the effects of stocking density and rainfall were examined with redundancy analysis.

Results: Vegetation cover, species richness and Shannon-Wiener index of diversity showed an increase and range condition improved with time. These positive changes could be related to the removal of high numbers of livestock and low wildlife numbers in the first years of survey. A gradual decline in the rate of increase in some of these parameters could be related to high grazing pressure during the later monitored years. There was a notable increase in non-succulent chamaephytes, but the initial increase in succulent chamaephytes was not sustained. The directional change evident in perennial species composition, supports the equilibrium concept, whereby the negative changes induced by heavy grazing were partially reversed. Within the directional change, four quasi-stable states could be distinguished, which could be reconciled with the state-and-transition model. The annual component showed no directional change, but displayed event-driven, non-equilibrium dynamics by fluctuating in reaction to the timing and quantity of rainfall.

Conclusions: The vegetation change displayed elements of both equilibrium and non-equilibrium dynamics, and demonstrated that the effects of heavy grazing in the Succulent Karoo were reversible. Overall, the recovery process proceeded slowly and was primarily detected in the perennial component of the vegetation. The increase in wildlife numbers in the later studied years and decline in perennial vegetation cover stress the need for active management of animal numbers to avoid vegetation degradation.

Introduction

In the Succulent Karoo, a global hotspot of biodiversity, heavy grazing is considered to be the greatest threat to the indigenous vegetation, and can lead to marked changes in species and life-form composition (Todd & Hoffman 1999; Haarmeyer et al. 2010).

The reversibility of vegetation change in arid rangelands is a key issue when considering options to restore degraded land. Many studies conducted in arid regions of southern

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Africa have shown that no improvement of the rangeland occurs after removal of livestock (Wiegand & Milton 1996; Jeltsch et al. 1997; Todd & Hoffman 1999). The two paradigms of vegetation dynamics hold opposing views on the question of reversibility. According to the equilibrium paradigm, vegetation change proceeds along a single, predetermined pathway, as defined by Clement's successional theory, and these changes are described as continuous and reversible. Systems displaying equilibrium dynamics are internally regulated and there is a tight coupling between plants and herbivores (Dijksterhuis 1949; DeAngelis & Waterhouse 1987). According to the non-equilibrium paradigm, vegetation change is driven primarily by climatic factors, and these external factors override the internal biotic controls and the coupling between plants and herbivores is weak (Ellis & Swift 1988; Behnke & Scoones 1993; Briske et al. 2003, 2005). A coefficient of variation in the annual rainfall of 33% has been proposed as the threshold above which non-equilibrium dynamics should prevail (Ellis & Swift 1988; Von Wehrden et al. 2012).

Despite the apparently contrasting attributes of these paradigms, it is currently accepted that they are not mutually exclusive and that neither of the two can fully explain the complex dynamics in arid rangelands on their own (Fernandez-Gimenez & Allen-Diaz 1999; Briske et al. 2003; Vetter 2005; Gillson & Hoffman 2007; Derry & Boone 2010; Sasaki 2010). Nevertheless, full integration between the two paradigms has not yet been achieved, and rangeland management seems to be progressing at the extremes of the equilibrium–non-equilibrium continuum (Todd & Hoffman 2009; Sasaki 2010). The two paradigms have far-reaching management implications. The equilibrium concept incorporates managerial involvement in the form of setting a carrying capacity for livestock or wildlife. In contrast, systems following non-equilibrium dynamics are often perceived as being insensitive to livestock impact and, consequently, strategies to manage (or reduce) stocking densities are considered unnecessary (Vetter 2005).

Studies on the effect of grazing pressure on species richness and diversity in the Succulent Karoo have shown variable responses. Several authors found no significant difference in species richness and/or diversity with increased grazing pressure (Todd & Hoffman 1999; Anderson & Hoffman 2007; Haarmeyer et al. 2010). However, Hendricks et al. (2005) reported a decline in species richness along a grazing intensity gradient, whereas Rutherford & Powrie (2010) reported an increase in species richness at higher grazing pressure.

Because vegetation change in arid ecosystems is often slow (Goldberg & Turner 1986; Wiegand et al. 1995; Wiegand & Milton 1996; Cody 2000; Lawley et al. 2013), data must be collected over decades to gain an understanding of how vegetation responds to short-term, inter-annual variation in rainfall; long-term cyclic rainfall patterns; episodic rainfall events; and grazing pressure (Kraaij & Milton 2006; Lindenmayer & Likens 2010). There is a dearth of long-term data on vegetation dynamics in the Succulent Karoo, with only three published studies: Jürgens et al. (1999) reported on dynamics in the Richtersveld over a 15-yr period; Rahlao et al. (2008) conducted a diachronic study with a survey interval of 67 yr; and Schmiedel et al. (2012) monitored vegetation change in the Knersvlakte over a 12-yr period.

Before the Goegap Nature Reserve (initially called Hester Malan Nature Reserve) was proclaimed, it had been heavily grazed with livestock (Le Roux 1984). The fencing of the reserve created an opportunity to investigate the vegetation dynamics after withdrawal of livestock and the eventual replacement of livestock with wildlife. At the same time, changes in life-form composition and species diversity could be studied to determine whether changes in the density and composition of the grazing guild were reflected in changes in life-form composition or diversity.

In this paper we report the changes in cover, species composition and diversity of the vegetation at two long-term monitoring transects over a period of 40 yr. The objectives of the study were to:

- establish whether any directional changes in species composition, life-form composition and diversity have occurred;
- determine whether these changes constituted an improvement in the range condition since the removal of livestock, or whether a permanent reduction in the biological potential of the land had occurred; and
- investigate the contributions of internal (wildlife grazing) and external factors (rainfall) on the vegetation change.

Study area

The Goegap Nature Reserve is situated ca. 15 km east of the town of Springbok in Namaqualand, in the north-western corner of the Republic of South Africa (Rösch 2001). It was established in 1966 and fenced in 1969 to exclude livestock that previously grazed freely on the land (Le Roux 1984).

Topographically, the reserve represents the characteristic Namaqualand landscape, with gneiss hills belonging to the Namaqua-Natal Metamorphic Province and sandy plains covered with early Tertiary to more recent deposits of sand. The vegetation on the hilly terrain is classified as the Namaqualand Klipkoppe Shrubland, whereas the plains support the Namaqualand Blomveld (Mucina & Rutherford 2006). Perennial plants are mainly summer-deciduous or evergreen, succulent dwarf shrubs. A prominent feature of the region is the extravagant spring floral

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display of winter-growing annuals (Van Rooyen 2002). However, due to the erratic nature of the rainfall, species composition and density of the annual plant populations vary from year to year, and a succession of specific environmental conditions is necessary for dense stands of annuals to develop (Van Rooyen et al. 1991, 1992).

The climate of the study area is characterized by low, unpredictable rainfall, falling mainly in winter. The mean annual rainfall recorded in the proximity of the sites since 1977 was 157 and 161 mm for the Tierkloof and Carolusberg transects, respectively (coefficient of variation of 40.1% and 39.6%, respectively).

Methods

Field survey

In 1974 two sites were selected for monitoring (Appendix S1), and 1-km transects were marked permanently at 100-m intervals with iron rods. Both transects are underlain by Nababeep gneiss of the Namaqua-Natal Metamorphic Province and occur at approximately the same altitude. The sites differ in that the Carolusberg transect falls within the Namaqualand Blomveld and occurs on the Ae80 Land Type, which contains red, high base status soils and occurs on footslopes and in valleys (Land Type Survey Staff 1987), whereas the Tierkloof transect falls within the Namaqualand Klipkoppe Shrubland and lies on the Ib127 Land Type with a 60–80% cover of rock, stones or boulders. Neither of the sites constitute prime habitat for plains wildlife such as gemsbok and springbok, however, the Carolusberg site is more accessible to plains wildlife than the Tierkloof site. In contrast, Hartmann's mountain zebra make more use of the Tierkloof site than the Carolusberg site.

Surveys were conducted annually (except for 1981, 1983, 1988, 1992) between 25 August and 7 September. The descending point method (Roux 1963) with 1000 points per survey was used to determine species composition and vegetation cover at each transect. The following data were recorded at each 1-m interval:

- first strike (foliar or canopy) = plant species first touched by the rod or within its canopy spread;
- second strike (foliar or canopy) = plant species growing beneath the first plant species and also touched by the rod or within its canopy spread.

Data analysis

The following values were calculated annually for each transect:

- vegetation cover = number of first strikes expressed as a percentage of the total number of possible strikes (1000);
- abundance per species = sum of first and second strikes;
- species richness (S) = total number of species recorded per transect;
- Shannon-Wiener index of diversity (H'; Krebs 1999).

To observe changes in the life-form composition, each species was assigned to a life-form category (Mueller-Dombois & Ellenberg 1974). The abundance per life form was calculated as the sum of first and second strikes.

Based on the short gradient lengths (Lepš & Šmilauer 2003), a linear model, principal coordinates analysis (PCoA), was selected as indirect ordination technique to illustrate the trajectories of the annual and perennial components at both sites. For the ordinations, performed in SYN-TAX 2000 (Podani 2001), the frequencies were standardized using a natural logarithmic ($\log_e$) standardization, and the Bray-Curtis measure was applied. Additionally, an incremental sum of squares cluster analysis (Ward's algorithm) was run on the floristic data in SYN-TAX 2000 using the log-transformed values and the Bray-Curtis measure (Podani 2001). The groups derived by the cluster analysis were delineated in the PCoA ordination.

A direct gradient analysis by means of redundancy analysis (RDA) (CANOCO v 4.5; Microcomputer Power, Ithaca, NY, US) was used to examine the effects of rainfall and stocking density on the vegetation. Stocking density was expressed as ha/Large Animal Unit (indicated as HA/LAU in ordinations) to accommodate the changing size of the reserve. Rainfall was broken down into different components to investigate the relationship between rainfall and vegetation parameters:

- Summer rainfall (SUMMER) represented the rainfall from September–December of the previous year plus January–February of the current year and was expected to have an effect on only the perennial species.
- Winter rainfall (WINTER) from March–August of the current year was expected to have a pronounced effect on the annual species. Rainfall occurring in March was included into winter rainfall in this study because the winter annual species can germinate after rainfall in March (Van Rooyen et al. 1992).
- Annual rainfall in this instance was the rainfall of the 12 mo (Sept–Aug) preceding the survey (ANNUAL).
- Previous winter rainfall (PREV WIN) represented rainfall from March–August of the previous year and was included because it could affect the size of the seed bank of annual species and has been reported to affect vegetation dynamics in the Succulent Karoo (Wiegand et al. 1995).

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To determine whether the changes occurring in the vegetation were positive or negative the range condition was assessed using the grazing index method of Du Toit (2000, 2003). 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, suitable for the Succulent Karoo (Lloyd 1996). To determine whether stocking density exceeded the capacity of the reserve, the range condition of each plant community was assessed and a weighting applied to each community to accommodate habitat preference and accessibility of the habitat for wildlife. Because wildlife cannot be managed as intensively as livestock, the stocking density of wildlife is generally taken as 70% of that calculated for livestock (Bothma et al. 2004). Information on wildlife numbers was obtained from internal annual reports of the Goegap Nature Reserve.

Curve fitting was conducted with the aid of Statistica v 11 (Statsoft, Tulsa, OK, US).

Results

Rainfall

The annual rainfall varied approximately five-fold from 60 to 303 mm rain at Tierkloof and approximately six-fold from 54 to 316 mm at Carolusberg (Fig. 1). Rainfall in the first 3 yr of survey was average or above average (data for 1974–1976 from the town of Springbok), after which there was a period up to 1988 with low rainfall (except for one or two years with above average rainfall). In the next 9 yr, up to 1997, annual rainfall was seldom below average, and the last 16 yr were characterized by fluctuating above and below average annual rainfall (Fig. 1).

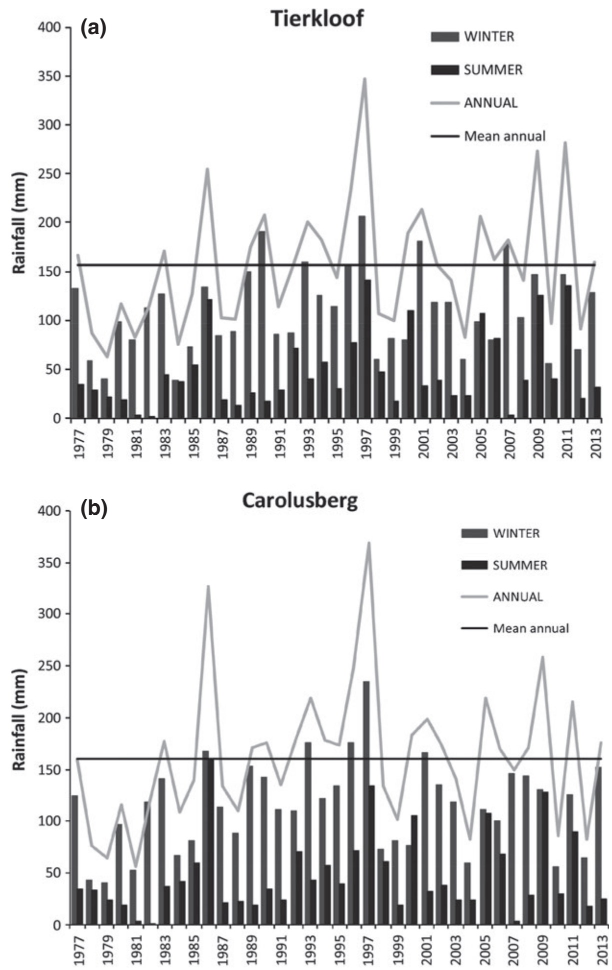

Fig. 1. WINTER, SUMMER, ANNUAL rainfall data (as used in ordinations) and mean annual rainfall at two sites (**a**. Tierkloof and **b**. Carolusberg) used for monitoring long-term vegetation change in the Goegap Nature Reserve.

Wildlife numbers

The first gemsbok (*Oryx gazella*) were introduced in 1970, with Hartmann's mountain zebra (*Equus zebra hartmannae*), springbok (*Antidorcas marsupialis*) and ostrich (*Struthio camelus*) introduced in 1973, 1974 and 1977, respectively. Animal numbers were initially kept low to allow the vegetation to recover after the decades of heavy grazing by livestock. In 1988, the Hester Malan Nature Reserve was enlarged and renamed the Goegap Nature Reserve, however, the fences on the eastern boundary were still kept intact. Around 1998 the capacity of the Hester Malan section of the reserve to sustain the number of animals it carried at that stage, had been reached (Fig. 2). In 2002, the fence between the Hester Malan section (ca. 6572 ha) and the neighbouring farm Goegap (ca. 8228 ha) was finally removed and the grazing pressure released. The increased size of the reserve was accompanied by an increase in animal numbers, especially gemsbok, which increased almost three-fold after 2004, but fell in 2008 and 2009 through the active removal of animals (Appendix S2).

The increased area available to wildlife after 2002 brought only temporary relief from the grazing pressure. As a result of the large increase in wildlife numbers, the stocking density of the reserve exceeded the capacity of the reserve to sustain the number of wildlife in some years, as was the case in 2007. In 2012, the farm Ratelkraal (8950 ha) was added to the reserve, which once again relieved the grazing pressure.

Canopy cover of perennial and annual species

At both sites total canopy cover revealed a significant, linear upward trend (Fig. 3a,b). Cover of the perennial species showed a logarithmic increase at Tierkloof (Fig. 3c),

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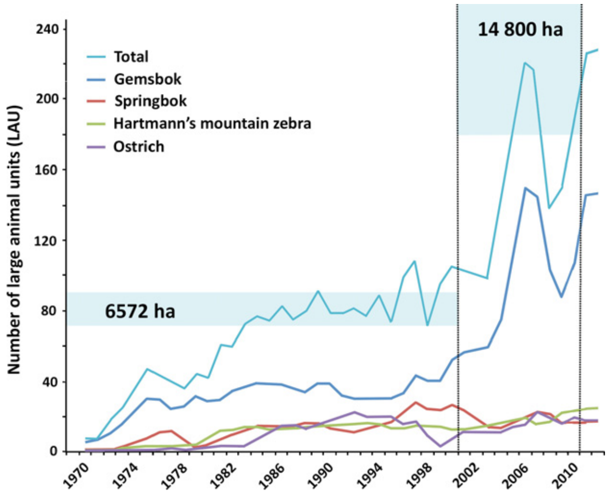

Fig. 2. Three-year moving average in gembok, springbok, Hartmann's mountain zebra and ostrich numbers (expressed as Large Animal Units) on the Goegap Nature Reserve. Shaded areas indicate bands between upper and lower thresholds of grazing capacity for high and low rainfall years, respectively. Dotted vertical lines indicate times when the size of the reserve was increased. See Appendix S2 for detail on animal removal activities.

whereas at Carolusberg, the initial increase in perennial species cover was followed by a decrease in the later years (Fig. 3d). In contrast to the cover of perennial species, the cover of annual species showed no directional trend (not shown). Contrary to what was expected, annual cover was not strongly correlated to any of the rainfall parameters.

Species abundance

The ten most abundant perennial species (first plus second strikes) at Tierkloof contributed to 82% of all strikes. Eight of these species showed an increase in abundance over time, whereas two species showed no directional trend (Appendix S3). None of the most abundant species at Tierkloof showed a decrease, however some of the less abundant species, in particular the succulent species, decreased markedly. The ten most abundant perennial species at Carolusberg contributed to 92% of all strikes. Six among these species showed an increase in abundance over the monitored period, two species decreased and no directional trend was observed for two species (Appendix S4). In general, annual species showed large fluctuations

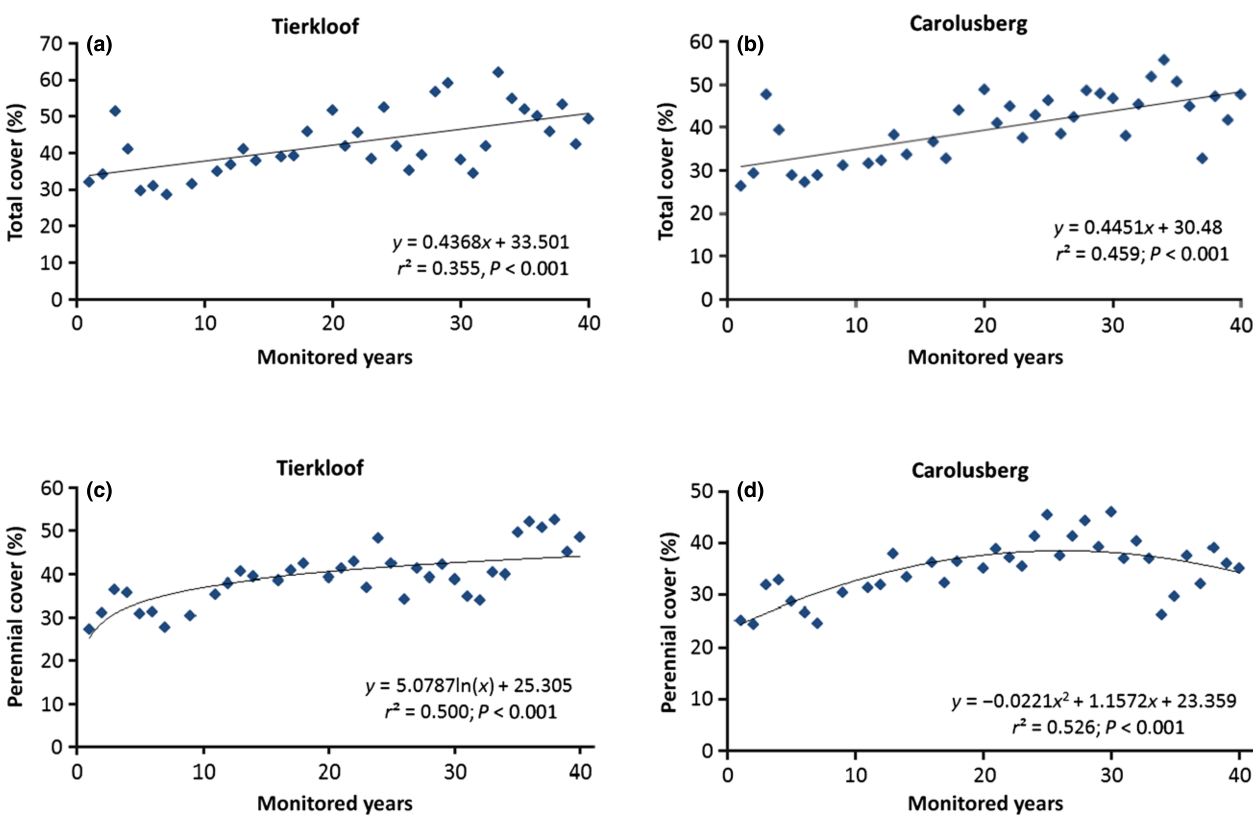

Fig. 3. Changes in total canopy cover (**a** & **b**) and canopy cover of perennial species (**c** & **d**) over a 40-yr monitoring period at two sites (Tierkloof and Carolusberg) in the Goegap Nature Reserve.

in abundance, with most species being recorded sporadically.

Species richness and diversity

The species richness of the perennial species increased at both transects during the monitored years (Fig. 4a,b). There was a weak, positive linear relationship between ANNUAL rainfall and perennial species richness at Tierkloof (r^2 = 0.169, P = 0.018) and with WINTER rainfall at Carolusberg (r^2 = 0.264, P = 0.002). At both sites the Shannon-Wiener index (H') mirrored the perennial species richness trends, indicating an overall increase in diversity of the perennial component (Fig. 4c,d). The species richness of the annual species revealed large fluctuations. There was a weak (significant only for Tierkloof) positive relationship between annual species richness and WINTER rainfall (Tierkloof: r^2 = 0.120, P = 0.048; Carolusberg: r^2 = 0.112, P = 0.081).

Life-form composition

There was a significant, linear increase in the abundance of non-succulent chamaephytes over the monitored period at both transects (Fig. 5), whereas the changes in succulent chamaephyte abundance were more complex. At both sites, the initial increase in succulent abundance was followed by a decrease, whereupon it increased again towards the end of the monitoring period at the Tierkloof site. Nanophanerophyte and geophyte abundances increased significantly, while therophyte, liana and parasite abundances showed no significant increase or decrease (Appendix S5). Hemicryptophyte abundance increased significantly only at Tierkloof.

Range condition

The range condition score for both sites showed a steady linear increase over time, indicating an improvement in the rangeland condition (Fig. 6). In general, the species with a high grazing value showed increases in abundance, whereas those with an intermediate and low grazing value increased, decreased or remained unchanged over the monitored period (Appendices S3, S4).

Floristic composition

A directional change in floristic composition of the perennial species was evident in the PCoA ordination of the floristic data at Tierkloof (Fig. 7a). The years were subdivided

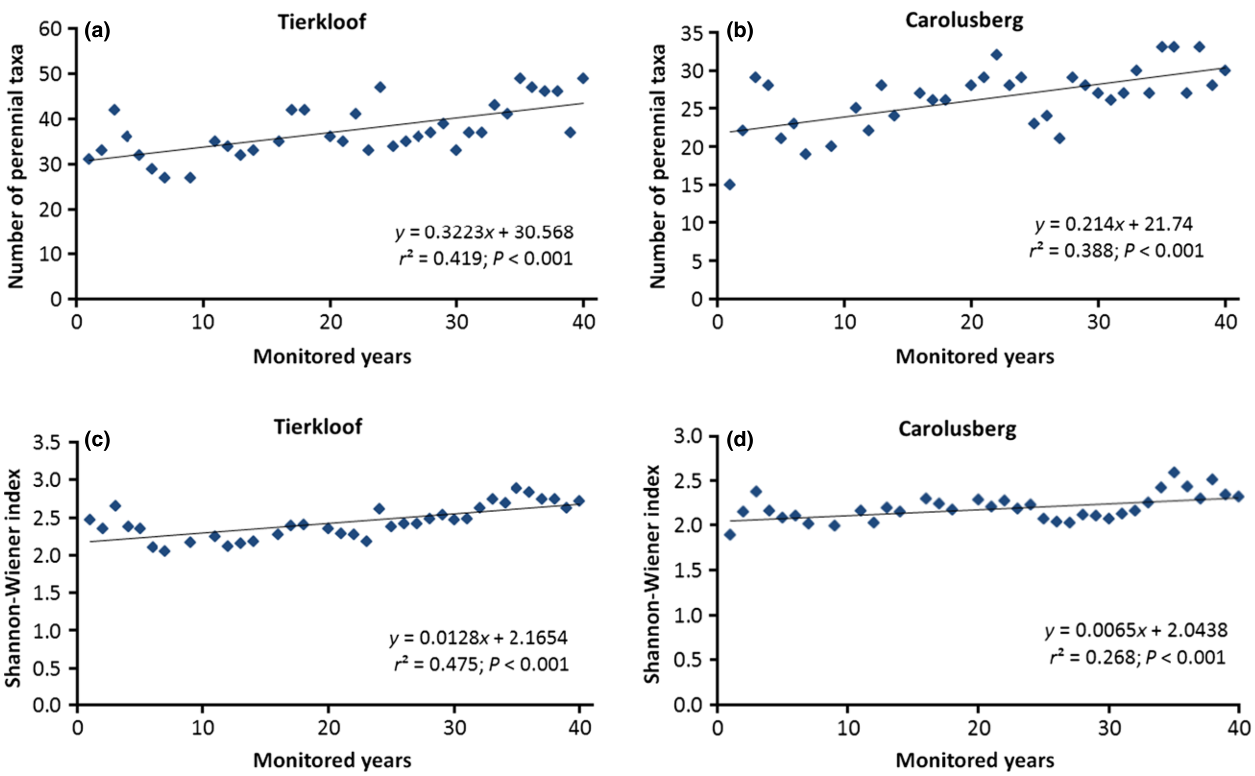

Fig. 4. Changes in perennial species richness (**a** & **b**) and Shannon-Wiener index (**c** & **d**) over a 40-yr monitoring period at two sites (Tierkloof and Carolusberg) in the Goegap Nature Reserve.

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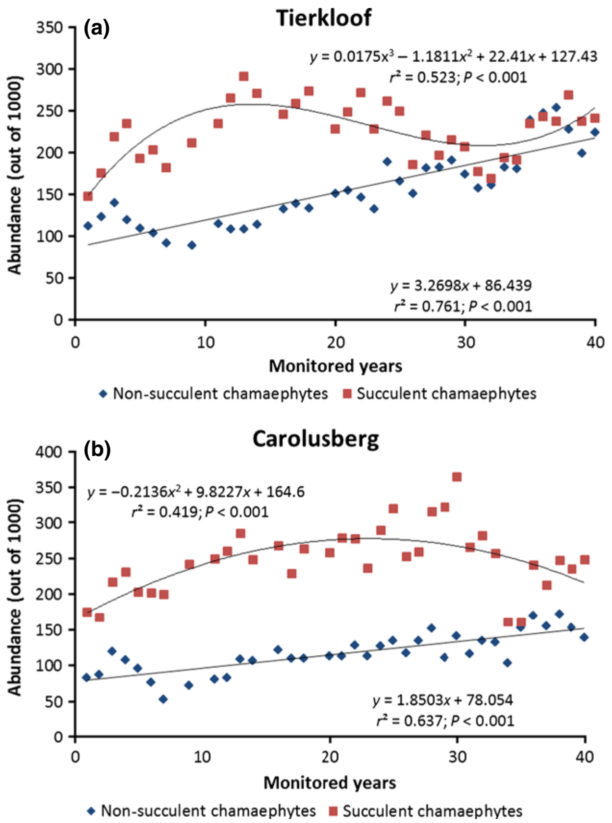

Fig. 5. Trends in abundance of succulent and non-succulent chamaephyte life forms over a 40-yr monitoring period at two sites (**a**. Tierkloof and **b**. Carolusberg) in the Goegap Nature Reserve.

into four clusters on the basis of the incremental sum of squares cluster analysis (Appendix S6). Overall, it appeared that there was a gradual progression from the poor condition in cluster 1 yr, to cluster 2. However, cluster 3 yr showed a slight retrogression, after which the progression continued in cluster 4 yr. The PCoA of annual species composition showed no directional change over the monitored years (not shown), but fluctuated in reaction to the timing and quantity of rainfall, and consequently years with similar rainfall patterns were grouped together.

At Carolusberg, the perennial species composition also revealed directional changes over the monitored years (Fig. 7b). There was a gradual progression from the poor condition in cluster 1 yr, through cluster 2 to cluster 3 yr, after which there was a marked retrogression to cluster 4 yr. Similar to what was found at Tierkloof, the annual species composition showed no directional change over time (not shown).

The percentage of total variability explained by all the environmental variables in the RDA of perennial species floristic data at Tierkloof and Carolusberg (Table 1, Appendix S7) indicated that stocking density was the best predictor of perennial species composition, with stocking density accounting for 48% and 27% of the total variability at the two sites, respectively. In contrast, stocking density was a poor predictor of annual species composition, accounting for 21% and 16% of the total variability explained by all environmental variables at Tierkloof and Carolusberg, respectively. At both Tierkloof and Carolusberg WINTER rainfall explained the most of the variability (37% and 24%, respectively; Table 1, Appendix S8).

Discussion

Canopy cover, life-form composition and diversity

In the Succulent Karoo, heavy grazing is known to lead to a reduction in vegetation cover and productivity (Todd & Hoffman 1999; Hendricks et al. 2005), and increases in cover following the withdrawal of livestock were reported in Kraaij & Milton (2006; Nama Karoo) and Rahlao et al. (2008; Succulent Karoo for off-heuweltjie sites). The increase in cover in the current study could therefore be related to the removal of livestock and low numbers of

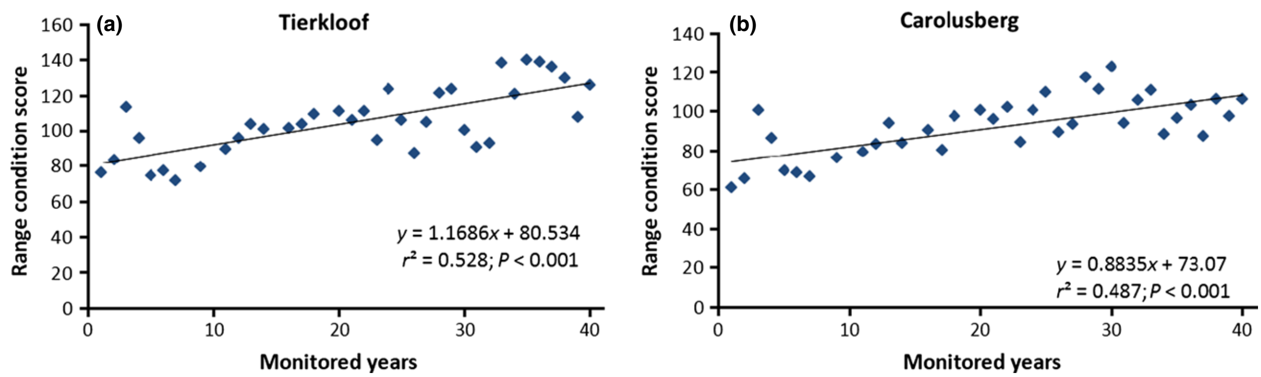

Fig. 6. Changes in range condition (following Du Toit 2003) over a 40-yr monitoring period at two sites (**a**. Tierkloof and **b**. Carolusberg) in the Goegap Nature Reserve.

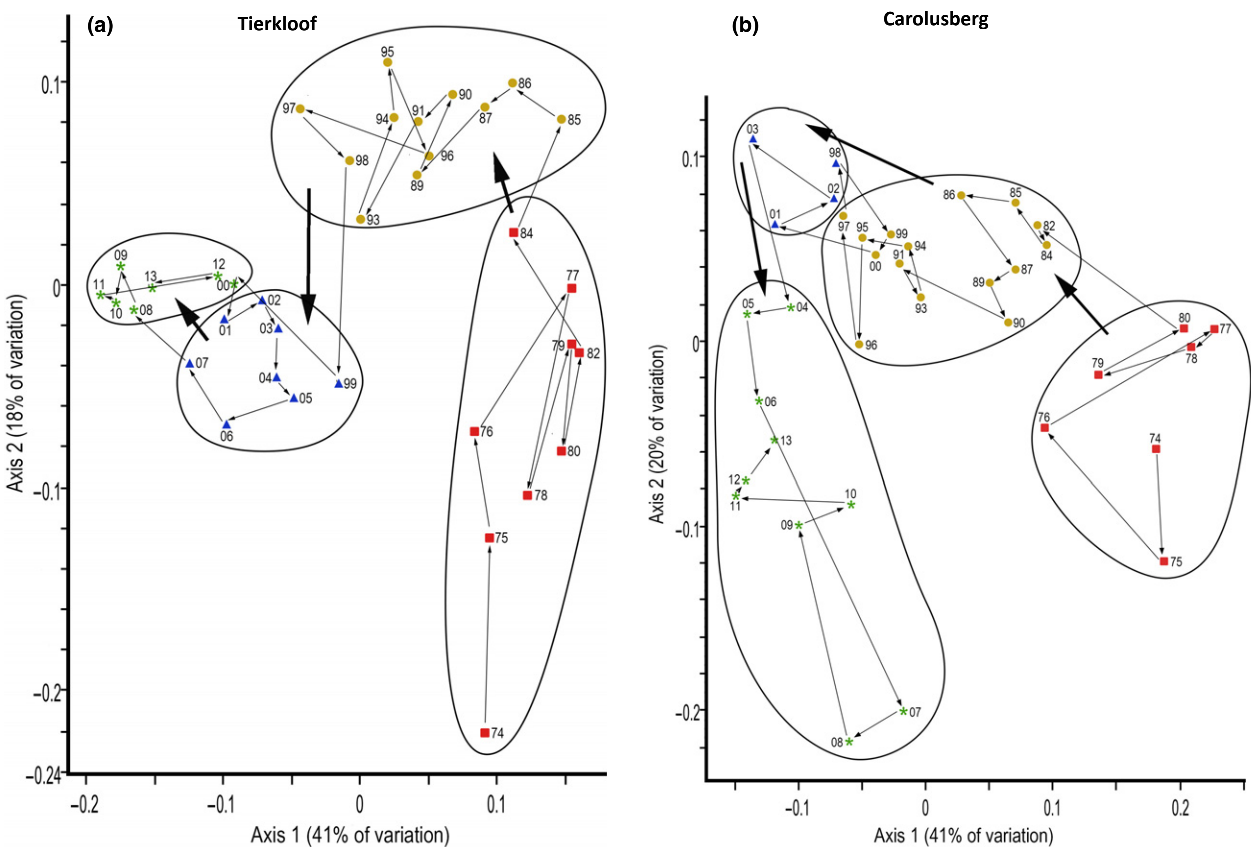

Fig. 7. Principal coordinates analysis scatter diagram of perennial species' floristic data at two long-term monitoring sites (**a**. Tierkloof and **b**. Carolusberg) in the Goegap Nature Reserve. Numbers indicate years, e.g. 74 = 1974 and 04 = 2004. Grouping is based on the incremental sum of squares cluster analysis (see Appendix S6).

Table 1. Variability accounted for by the individual environmental variables as a percentage of total variability explained by all the environmental factors, derived from redundancy analysis at two long-term monitoring sites (Tierkloof and Carolusberg) in the Goegap Nature Reserve.

Environmental variable	Variability accounted for by the environmental variables (%)			
	Perennial species		Annual species	
	Tierkloof	Carolusberg	Tierkloof	Carolusberg
Stocking density (ha/LAU)	48	27	21	9
Annual rainfall (mm)	35	16	25	11
Summer rainfall (mm)	30	13	22	20
Previous winter rainfall (mm)	24	23	19	21
Winter rainfall (mm)	19	22	37	24

wildlife in the first years of survey. However, perennial cover at Tierkloof showed a gradual decline in the rate of increase (Fig. 3c), whereas perennial cover at Carolusberg decreased in the second half of the monitored period (Fig. 3d). These decreases could possibly be related to the high numbers of wildlife in this period.

Heavy grazing in the Succulent Karoo is generally associated with changes in species and life-form composition resulting in an increase in annual, unpalatable perennial, or geophytic species at the cost of palatable perennial species (Todd & Hoffman 1999, 2009; Hendricks et al. 2005; Anderson & Hoffman 2007; Rutherford & Powrie 2010). In the current study, no trends were observed for the annual and geophytic life forms, but the non-succulent chamaephytes showed a marked increase in cover upon removal of livestock. Within this life form, an increase in highly palatable species, e.g. *Tripteris sinuata* and *Hirpicium alienatum*, occurred and consequently the range condition score also revealed a steady increase. Although the abundance of succulent chamaephytes initially increased, this increase was not sustained and was followed by decreases at both sites. Overall, the succulent species had intermediate to low grazing values and although there were some succulent species that increased over the monitored period, many of them showed no overall increase and many

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declined. A decrease in succulent cover was also reported in Rahlao et al. (2008) after removal of livestock.

Total and perennial species richness increased significantly over the 40-yr period, corresponding to the trends reported in Kraaij & Milton (2006; Nama Karoo), Rahlao et al. (2008) and Lawley et al. (2013; South Australia) when grazing pressure is reduced.

Directional trends

Many studies conducted in arid regions have shown that no improvement of the rangeland occurs after removal of livestock due to demographic inertia and lag effects (Wiegand et al. 1995; Jeltsch et al. 1997; Todd & Hoffman 1999). In their model, Wiegand & Milton (1996) predicted that no improvement was likely even after 60 yr of withdrawal of livestock. This gloomy prediction was not supported by the current study. A clear directional change in perennial species composition from the earlier to the more recent years was evident at both sites. Considering the improvement in range condition that occurred during this period, the change in species composition is seen as positive. These directional dynamics support the equilibrium concept, whereby progressive succession occurs after removal of livestock, with the system returning to a more 'healthy' state.

Four more of less successive groups of years could be distinguished within the gradual directional change occurring at both sites. These groups could possibly be interpreted as quasi-stable states according to the state-and-transition model. At both Tierkloof and Carolusberg, the first two transitions could be linked to low rainfall. At Tierkloof the third transition appeared unrelated to rainfall, but coincided with a sudden sharp increase in wildlife numbers (cluster 3 in Fig. 7a). The rocky valley at Tierkloof is used by Hartmann's mountain zebra as well as plains wildlife (although not preferred by the latter). After the animal removals in 2008 and 2009 the grazing pressure at the Tierkloof site was reduced and a gradual improvement was once more noticed (cluster 4, Fig. 7a). The vegetation at Carolusberg was slower to respond to the increasing grazing pressure (cluster 4, Fig. 7b), and even after the animal removals, no further transition has occurred.

It has been suggested that in arid regions severe drought leads to large-scale mortality, which then opens up space for large recruitment events (Goldberg & Turner 1986; Turner 1990; Wiegand et al. 1995; Agnew 1997; Milton & Dean 2000). The fact that the first two transitions coincided with below-average rainfall periods could lend some support to the presence of establishment surges after periods with below-average rainfall. However, many other studies in arid regions have reported no strong relationship between rainfall and canopy cover, and indicated that mortality and recruitment were not episodic (Jürgens et al. 1999; Anderson & Inouye 2001). In the current study, the relationship between rainfall and cover of perennial species was low, supporting the contention of Jürgens et al. (1999) and Watson et al. (1997) that opportunities for recruitment are available every year and that small continuous background processess occurring in the same direction could be as important as large episodic events (Watson et al. 1996).

Equilibrium and non-equilibrium dynamics

Based on the CV of rainfall, which exceeds 33%, non-equilibrium dynamics were expected in the study area, and consequently it was predicted that the coupling between plants and herbivores would be weak and that vegetation change would be driven primarily by external climatic factors. These predictions did not hold true for the perennial component, where continuous directional change occurred (Fig. 7) and grazing pressure, as an internal biotic control, was most important for vegetation dynamics (Table 1). This supports the viewpoint of Todd & Hoffman (2009) that there is a close relationship between livestock numbers and primary production in Namaqualand and that the typical non-equilibrium dynamics associated with the arid and semi-arid grasslands of East Africa and the Sahel (Ellis & Swift 1988) are not in accord with the dynamics in the Succulent Karoo shrubland in South Africa (Todd & Hoffman 2009).

In semi-arid environments in South Australia, Lawley et al. (2013) also contended that internal factors are more important drivers of community assembly than external climatic factors. As far as the perennial component of the vegetation is concerned, internal biotic controls seemed to override external factors in the current study, and the importance of internal processes, such as population dynamics (Conradie & Van Rooyen 2005), dispersal (Van Rooyen et al. 1990), competition (Oosthuizen et al. 1996; Rösch et al. 1997; Carrick 2003) and facilitation (Eccles et al. 1999; De Villiers et al. 2001) in the Succulent Karoo have all been well documented.

The annual vegetation component showed large temporal fluctuations in cover, species richness and composition; the last could be related to the timing and amount of rainfall. These fluctuations in response to rainfall have been described as event-driven, non-equilibrium dynamics (Westoby et al. 1989; Behnke & Scoones 1993; Wiegand & Milton 1996).

Conclusions

Long-term ecological monitoring is generally the preferred method for detecting changes in slow phenomena, subtle and complex phenomena and episodic or rare events. In the Goegap Nature Reserve vegetation cover, species richness and Shannon-Wiener index of diversity showed an increase and range condition improved with time. Life-form composition also changed, with the increase in non-succulent chamaephytes being the most notable.

The vegetation change illustrated in this study displayed elements of both equilibrium and non-equilibrium dynamics. The directional change in the composition of perennial species over the monitored years was evidence of the occurrence of equilibrium dynamics. Furthermore, a relationship between stocking density (internal factor) and perennial species composition could be demonstrated. Yet, even within the gradual directional change, quasi-stable states could be distinguished, which could be reconciled with the state-and-transition model of vegetation dynamics. The annual component displayed clear non-equilibrium dynamics, with rainfall (external factor) having the largest effect.

Of great importance is that the results showed that the effects of heavy grazing before the proclamation of the reserve were not irreversible, and that a permanent reduction in the biological potential had not occurred. Overall, the recovery process proceeded very slowly and was primarily detected in the perennial component of the vegetation, with the annual component reacting to rainfall. The increase in wildlife numbers in the latter studied years and decline in perennial vegetation cover, highlight the fact that animal numbers on the reserve will have to be actively managed to avoid degradation of the vegetation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location of the Goegap Nature Reserve and the two long-term monitoring transects within the reserve.
Appendix S2. Animal introduction/removal activities on the Goegap Nature Reserve.
Appendix S3. Changes in abundance of the ten most abundant species at the Tierkloof transect over the 40-yr monitoring period.
Appendix S4. Changes in abundance of the ten most abundant species at the Carolusberg transect over the 40-yr monitoring period.
Appendix S5. Relationships between abundance of various life forms and time.
Appendix S6. Cluster analysis of perennial species' floristic data.
Appendix S7. Redundancy analysis of perennial species' floristic data against environmental variables.
Appendix S8. Redundancy analysis of annual species' floristic data against environmental variables.

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