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Changes
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Assessments, changes, challenges, and solutions

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Vegetation dynamics in the Namaqualand Hardeveld — observations from 17 years of annual monitoring

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Abstract: Rangelands in arid areas of southern Africa are prone to degradation through overutilization. Once degraded, rangelands recover very slowly or may not recover without external drivers such as very high-rainfall years. To what extent, at what pace, and to which state Succulent Karoo vegetation is able to recover from long-term exposure to high grazing pressure — from extensive commercial farming, for instance — is poorly understood. We analysed 17 years of annual vegetation monitoring data from the Hardeveld bioregion of the South African Namaqualand. The recording commenced one year after the grazing pressure on the rangeland had been reduced from as much as 120% to 30% of the recommended stocking rate. Non-metric multidimensional scaling (NMDS) of all 17 annual relevés for the 20 plots showed a strong division of the species composition into 8 upland and 12 lowland plots. When applying NMDS to the relevés for the plots separately, in comparison with the lowland plots, upland plots showed a stronger directional change where the species composition shifted away from the initial state. The year-to-year species turnover per habitat, however, was greater on lowland compared to upland habitats. The visualisation of the cover changes per life form type showed that both habitats differed in their life form composition, with a higher dominance of large shrubs in upland compared to lowland habitats. The outcome of the study revealed a habitat-specific response of vegetation to land use change. But even within the habitats, the vegetation showed plot-specific responses of the vegetation to the variances in abiotic factors. We suggest that further analyses should have a stronger focus on species-specific responses at the different sites and employ a more refined life form classification, adapted for the Succulent Karoo vegetation.

Resumo: As pastagens em áreas áridas do Sul de África têm tendência a serem degradadas pela utilização excessiva. Uma vez degradadas, as pastagens recuperam muito lentamente ou podem não recuperar sem factores externos, tais como anos de chuva intensa. Sabe-se pouco sobre até que ponto, a que ritmo e a que estado a vegetação de Succulent Karoo é capaz de recuperar de uma exposição de longa duração a uma alta pressão de pastoreio, por exemplo de agricultura comercial extensiva. Analisámos 17 anos de dados de monitorização anuais de vegetação da bioregião de Hardeveld, da Namaqualand da África do Sul. O registo foi iniciado um ano após a redução da pressão de pastoreio, de 120% para 30% da taxa recomendada de densidade. O escalonamento multidimensional não-métrico (NMDS) de todos os 17 relevés anuais para as 20 parcelas mostrou uma forte divisão da composição específica em oito parcelas de montanha e doze parcelas de planície. Quando o NMDS foi aplicado aos relevés para as parcelas em separado, em comparação com as parcelas de planície, as de montanha mostraram uma mudança direccional mais forte onde a composição de espécies se afastou do estado inicial. Porém, o *turnover* the espécies anual por habitat foi maior em habitats de planície, em comparação com habitats de montanha. A visualização das alterações de cobertura por tipos de formas de vida mostrou que ambos os habitats variaram na sua composição de formas de vida, com uma maior dominância de grandes arbustos nos habitats de montanha, em comparação com os habitats de planície. O resultado do estudo revelou uma resposta da vegetação específica ao habitat em relação à alteração do uso das terras. Mas, mesmo dentro dos habitats, a vegetação mostrou respostas específicas aos plots em relação à variação dos factores abióticos. Sugerimos que futuras análises tenham um foco mais forte nas respostas específicas das espécies nos diferentes locais, e empreguem uma classificação de formas de vida mais refinada, adaptada à vegetação de Succulent Karoo.

Introduction: why do we do long-term monitoring in SASSCAL?

The main land use in southern African drylands is rangeland farming — that is, the use of the natural vegetation as a grazing resource for livestock. The selective grazing behaviour of livestock favours the establishment of unpalatable species. This ultimately leads to a vegetation state that is less suitable for livestock. In the Succulent Karoo biome of southern Africa, selective grazing typically results in sparse vegetation dominated by unpalatable shrubs such as *Galenia africana* (Aizoaceae) and *Pteronia pallens* (Asteraceae), while during the growing season, annuals and geophytes fill in the vegetation gaps (Milton et al., 1994; Milton & Hoffman, 1994; Todd & Hoffman, 1999). Overgrazed rangelands that have reached this degraded vegetation state are less productive and prone to soil erosion, which leads to further degradation of the vegetation. Rangeland ecological concepts that help explain the drivers of vegetation degradation or of recovery are of high scientific and applied relevance.

One of the established concepts in rangeland ecology assumes that the rangeland condition and herbivores are in equilibrium and that vegetation changes are in direct response to herbivore pressure (equilibrium theory of the Clementsian concept). This concept, however, has been questioned for drylands, which exhibit a high variability in rainfall, and the non-equilibrium theory for these rangelands has been put forward (Ellis & Swift, 1988). According to the non-equilibrium theory, rangelands do not necessarily change back to the pre-disturbed state after the livestock pressure has been removed but require abiotic events such as high-rainfall seasons to trigger a vegetation transition to another state (Illius & O'Connor, 1999; Vetter, 2005; von Wehrden et al., 2012). Support for the non-equilibrium theory has been found for the rangelands of the Succulent Karoo (Milton et al., 1994). Results from other studies, however, suggest that biotic factors can well result in a shift in Succulent Karoo vegetation to a less degraded state (Rahlao et al., 2008; van Rooyen

et al., 2015). It has therefore been suggested that neither of the two concepts can explain the complex dynamics of arid rangelands exclusively (Gillson & Hoffman, 2007; van Rooyen et al., 2015).

This study will contribute to the understanding of the vegetation dynamics by analysing 17 years of annual permanent plot data from an arid winter rainfall rangeland in southern Africa (Haarmeyer et al., 2010) and focuses on the Namaqualand Hardeveld bioregion within the western Succulent Karoo (Mucina et al., 2006). The undulated landscape of Namaqualand is structured into relatively level lowland habitats and rockier, steeper upland habitats (Desmet, 2007). Lowland habitats, which are more accessible to livestock, tend to be more affected by grazing compared to upland habitats (Riginos & Hoffman, 2003; Anderson & Hoffman, 2007).

The camp studied at Soebatsfontein was used intensively for livestock farming over at least two decades until the year 2000, when the land was handed over to the Soebatsfontein community to be used as communal farmland. With the tenure change, the land use intensity changed from a high to a moderate intensity (Schmiedel et al., 2016). The Soebatsfontein communal farmers who farm in that particular camp take pride in farming sustainably (no overstocking, regular resting periods for the veld, etc.). Our monitoring of the plant communities started in 2001, one year after the land tenure change. By analysing the vegetation change over time, we aim to answer the following research questions:

1. Did the change in land use intensity lead to a detectable change in vegetation after 17 years?
2. Is there evidence of a habitat effect in the interannual vegetation variance between upland and lowland habitats of the Soebatsfontein study site?

What did we do and how?

Study site

The study site is located on the farm Kateklip, which forms part of the communal farmland of the Soebatsfontein community (NW corner, -30.1865° to

-30.1954° S, 17.54337° to 17.5538° E), at the foothills of the Kamiesberg escarpment in the Northern Cape Province of South Africa. The altitude ranges from 260 m to 435 m above sea level. The climate is characterised by little winter rainfall, with about 130 mm of precipitation per year (Haarmeyer et al., 2010). The mean annual temperature is 17.8°C , with extremes ranging from a minimum of 3.5°C in winter to a maximum of 42.4°C in summer (Haarmeyer et al., 2010). Soils are mainly durisols, cambisols and leptosols derived from a parent material of gneisses (Petersen, 2008). According to Mucina et al. (2006), the area is part of the Namaqualand Heuweltjieveld vegetation unit (SKn 4) within the Hardeveld bioregion of the Succulent Karoo biome. The study site is dominated by succulent dwarf shrubs, mostly from the families Aizoaceae and Crassulaceae (Luther-Mosebach et al., 2012). Mass flowering of annuals (mainly Asteraceae) occurs following the winter rainfall season.

The typical land use at the study site is small-stock farming with sheep and goats. Until 1999 the farmland was owned and managed by the South African diamond mining company De Beers and used for livestock farming. During at least the last two decades of that period, the land was used intensively and stocking rates reached between 80% and 120% of the recommended stocking rate of 9 ha/SSU (Schmiedel et al., 2016). In the year 2000, the farmland was handed over to the about 300 people of the Soebatsfontein community and has since been managed as communal rangeland (Schmiedel et al., 2010). Owing to financial constraints and a conservative farming approach by the responsible farmers, the stocking rate in that particular camp since 2000 has remained below 30% of the recommended stocking rate (Schmiedel et al., 2016).

Study design and data collection

The sampling methodology follows the standardised Biodiversity Observatory design (Jürgens et al., 2012) for long-term biodiversity monitoring. The permanently marked Biodiversity Observatory Soebatsfontein S22 (www.SASSCALObservationNet.org; Hillmann et al., 2018) is

1 km² in size and subdivided into a grid of 100 one-hectare plots. Twenty of the hectare plots were randomly selected using habitat stratification to ensure that all habitat types that occur in the observatory are included in the selection. In the centre of each selected hectare, a 10 m x 10 m plot was permanently marked. For these 20 plots, annual surveys (called *relevés* throughout the text) were conducted from 2001 to 2017 in July or August, which is the main growing season. In each *relevé* an estimation of the cover (0.01% to 100%) for each vascular plant species was made. Altitude, steepness of slope, and percentage of rock cover per plot were assessed once to describe the habitat characteristics of the plots. Weather data were recorded by the automatic weather station adjacent to Observatory S22 (−30.18294 S, 17.55062 E; see also ‘Soebatsfontein’ at www.SASSCALweathernet.org; Hillmann et al., 2018).

Data analyses

To identify high- and low-rainfall years, we visualised the interannual variance in the rainfall patterns by plotting the total annual rainfall over the study period in relation to the mean annual rainfall based on the 17 years of recording. We were interested in the general pattern of the species composition to distinguish major habitat types. For that purpose, we visualised the underlying vegetation pattern in the 20 plots by employing an ordination based on non-metric multidimensional scaling (NMDS). The ordination situates the *relevés* per plot for each of the 17 survey years into a multidimensional space based on their dissimilarity in terms of species composition. The measure of dissimilarity used was the Bray-Curtis distance measure. The more similar the species composition was, the closer the plots were arranged together. We fitted the environmental variables of altitude, slope, and rock cover into the ordination. The fitted environmental variables were correlated with the vegetation ordination at a significance level of $p < 0.05$. The observed divide of the vegetation data into the two main groups (i.e., upland and lowland habitats) enabled us to split the dataset accordingly and analyse the habitat-specific changes in the vegetation.

The species richness in the observatory (350 species per km²) was too high to analyse the vegetation changes at a species level. To reduce the complexity of the dataset, we grouped the species into major strategy types, so-called plant life forms (Raunkiaer, 1937). Plant life forms are defined based on their strategies to survive periods of adverse environmental conditions — in this case, the dry summer season in the Succulent Karoo. Annual plants (or ‘therophytes’), for instance, complete their lifecycles within one growing season and survive the dry period as seeds. Bulbous plants (or ‘geophytes’) completely withdraw during the dry period into the bulb or tuber. Perennial forbs or perennial grasses (‘hemicryptophytes’) reduce the above-ground biomass to a clump of culms or a rosette of leaves and regrow from buds near the soil surface. The architectures of the dwarf shrubs (‘chamaephytes’) and tall shrubs and trees (‘phanerophytes’) remain largely unchanged over the dry period; some of them shed their leaves or even branches, but they continue growing from their remaining branches during the next growing season. These plant life forms have different abilities to respond to environmental variances. Therophytes and geophytes respond strongly to rainfall and thus produce a lot of clutter in the dataset that does not necessarily explain a general trend. We therefore excluded all therophyte and geophyte species from the subsequent analyses. As a result, our analyses focused on perennial life form types such as chamaephytes, phanerophytes, and hemicryptophytes that are visible throughout their entire life span and, if they die, need several years to grow back to a mature stage.

We were interested in changes in the perennial species composition of the vegetation over the study period. Since the species composition varied strongly among the plots, we calculated separate NMDS ordinations for the 17 *relevés* for each of the 20 plots, again using the Bray-Curtis distance measure for the dissimilarity. To visualise the changes in the species composition from year to year, the *relevés* were connected by a vector chronologically.

To determine the rate at which perennial species in lowland and upland habi-

tats appeared or disappeared from year to year, we calculated their turnover rate. Finally, we analysed the change in the composition of perennial life forms per habitat type by employing rank clocks, where the interannual changes in vegetation cover per life form were displayed clockwise. We used the following life form types: H = hemicryptophytes, C_{mac} = macro-chamaephytes (30–50 cm height), C_{mes} = meso-chamaephytes (15–30 cm), C_{mic} = micro-chamaephytes (5–15 cm), C_{nano} = nano-chamaephytes (0–5 cm), P_{nano} = nano-phanerophytes (50–100 cm).

Results

The interannual variation of the annual rainfall varied between 50% (in the years 2015 and 2017) and 150% (2006, 2011, 2013, and 2016) of the mean annual rainfall of 130 mm (Fig. 1). The mean species richness per plot for a given year varied between < 20 (in 2017) and 40 species (in 2015). Species richness was not closely linked to total annual rainfall. Some years of low annual rainfall had high species numbers (e.g., 2015), and years with high annual rainfall had low species numbers (e.g., 2011) per plot.

The NMDS ordination grouped the 20 plots comprising 17 annual *relevés* each into two main groups arranged along the NMDS1 axis (Fig. 2). The smaller group to the left-hand side of the ordination was positively associated with the environmental variables altitude, slope, and rock cover and comprised the *relevés* of the eight upland plots. The other group comprised 12 lowland plots. In both habitat types the *relevés* per plot were clustered together in ordination space (Fig. 2). For the upland plots the *relevés* per plot were closely adjacent and overlapped only marginally, whereas the *relevés* per plot of the lowland were partly overlapping broadly.

Long-term shifts in species composition per plot were investigated by removing the opportunistic annuals and geophytes, which respond to the amount of seasonal rainfall rather than to long-term changes. Since the overall ordination (Fig. 2) showed that the vegetation

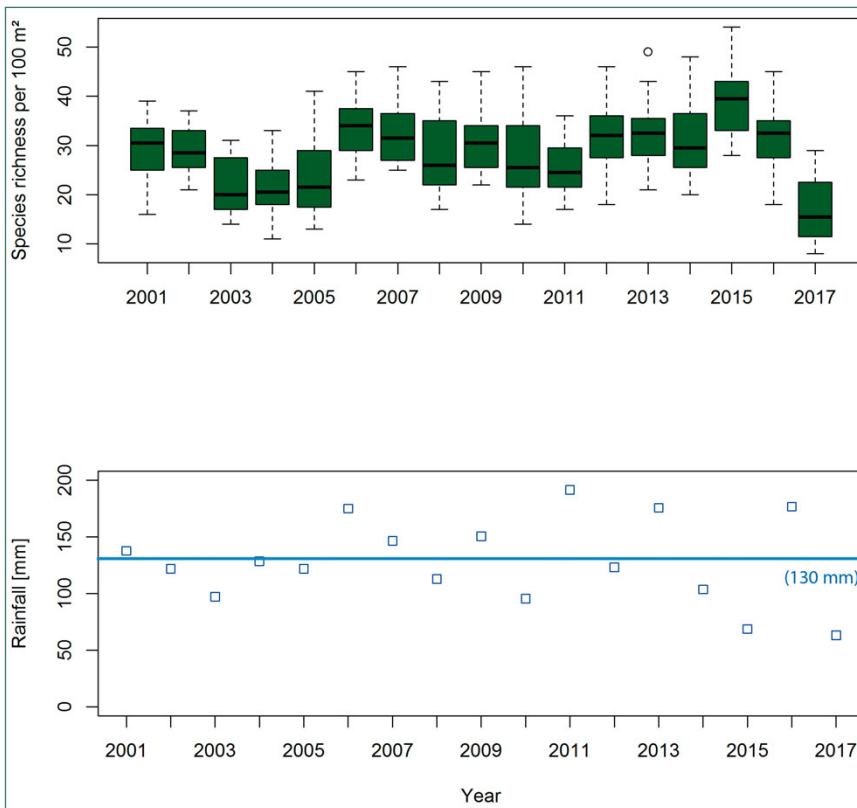


Figure 1: Above: Box plots showing the species richness of the twenty 100 m² plots per year. Bold black line: mean value; green box = 50% variance; hinges = highest and lowest quartile; dot = outlier. Below: Total annual rainfall for the 17-year study period at Soebatsfontein. Horizontal line indicates mean annual rainfall at 130 mm.

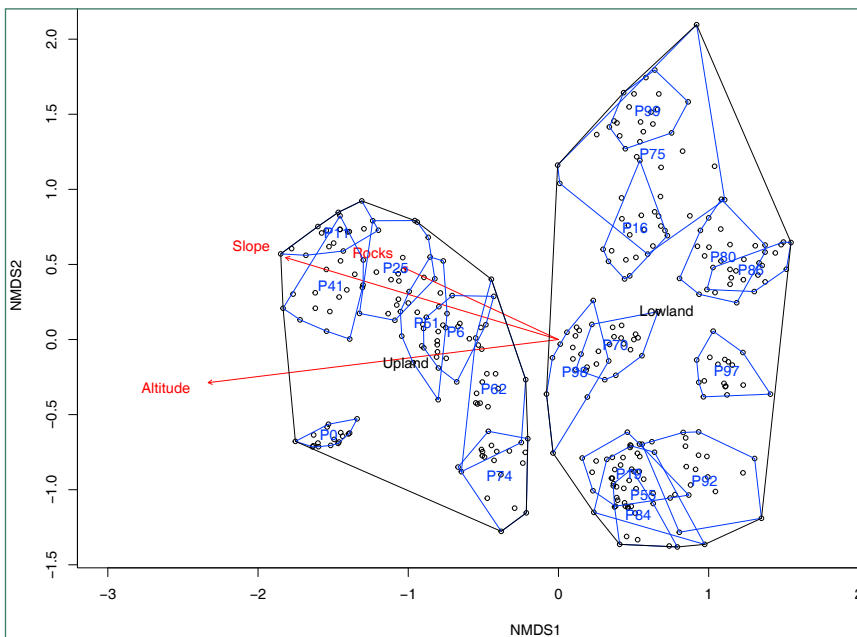


Figure 2: Non-metric multidimensional scaling (NMDS) ordination of 17 relevés of the 20 plots based on all species and three environmental variables, with a significant explanation for the dissimilarity in the species dataset ($p < 0.05$). Slope = slope in %; Altitude = meters above sea level; Rocks = total cover of rocks > 60 cm in diameter. Groups of lowland and upland plots are indicated by black hulls. Relevés belonging to the same plot were surrounded by blue hulls. Measure for dissimilarity was calculated using the Bray-Curtis distance measure.

of most of the plots was quite distinct, we analysed the vegetation changes for each plot separately by employing NMDS or-

dinations. The position of a relevé in the NMDS ordination space in relation to the other relevés indicates their dissimilarity

in species composition. The relevés were connected by a vector following their chronological sequence; the first year of the time series, 2001, was marked with a triangle, and the last year, 2017, was marked with an arrowhead. In this way, the direction of change of the vegetation between relevés for each plot from year to year was visualised. Beyond their interannual oscillations, the movement of the plots showed different patterns (Fig. 3 and 4). Some of the plots showed a directional shift to the right (red arrows), others moved in a semicircle (green arrows), and still others showed change of ambiguous direction (dark red arrows) or even a full circle (blue arrows). Of the 8 upland plots, 5 plots showed a directional change, 2 plots a semicircle, and 1 a full circle whereas among the 12 lowland plots the majority (9 plots) moved either in a semicircle (6 plots) or without a clear direction (3 plots) and only 2 plots showed a directional change.

The interannual appearance, disappearance, and total turnover rates for perennial species on lowland habitats varied more than on upland habitats. The appearance rates on lowland plots ranged from 2% to 17% compared to only 4% to 12% at the upland plots, and the disappearance rates ranged from 3% to 16% on lowland plots compared to 3% to 9% on upland plots (Fig. 5). The total species turnover rate ranged between 8% and 27% at the lowland plots compared to 11% and 21% at the upland plots. The peaks for appearance and disappearance were not synchronised between the habitat types, and the highest peaks of the appearance rate were not related to above-average annual rainfall but seemed to respond with a lag phase of one year.

Lowland and upland habitats differed not only in their species turnover rate but also in their life form composition (Fig. 6). Upland habitats were dominated by nano-phanerophytes and mesochamaephytes, whereas nano-chamaephytes and hemicryptophytes appeared at much lower rates than in the lowland habitats. The interannual variance between the perennial life forms in the two habitat types also differed. In the upland habitats, the less dominant life forms tended to oscillate more strongly between

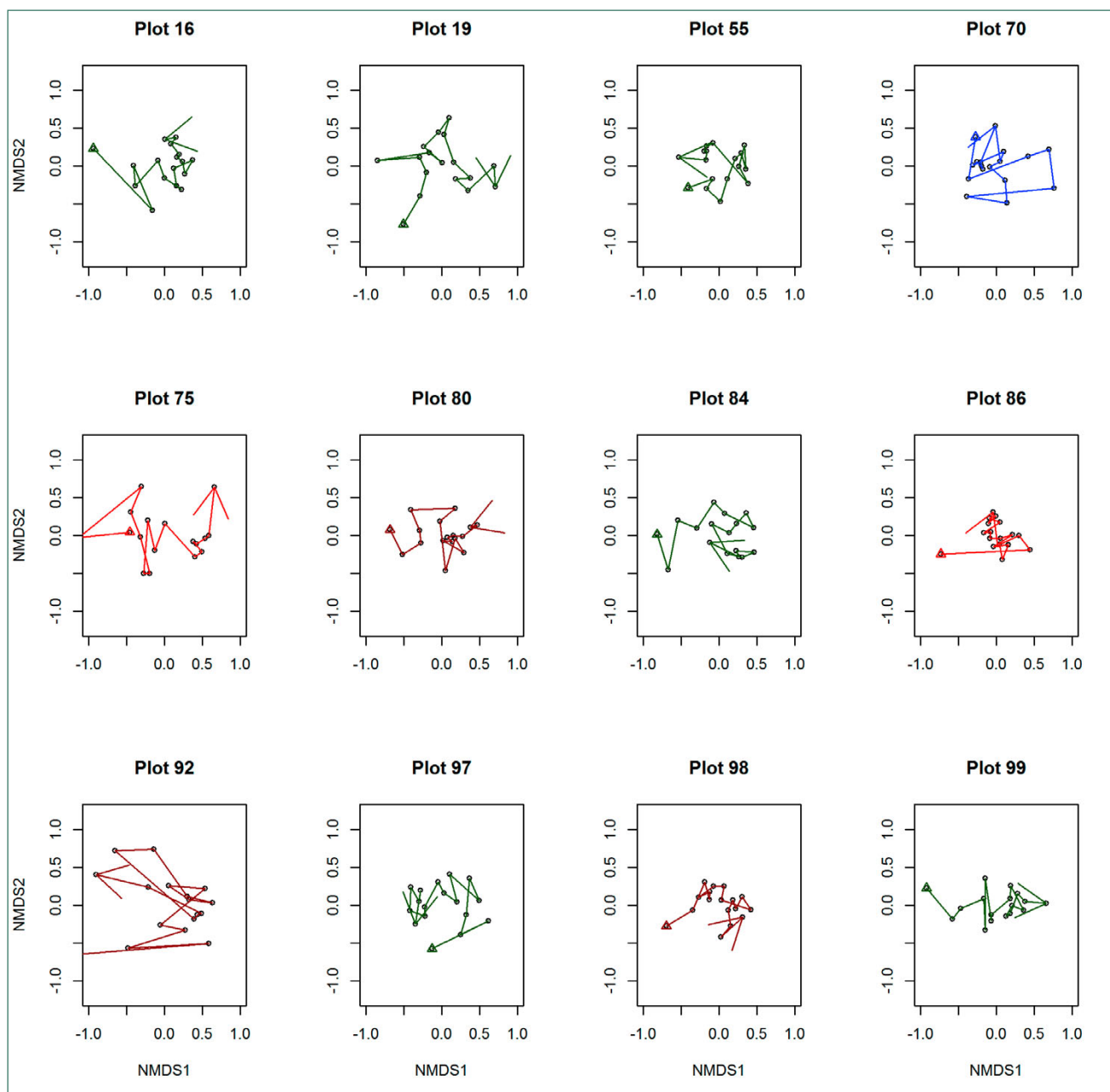


Figure 3: Non-metric multidimensional scaling (NMDS) ordination of the twelve lowland plots based on perennial species composition. A vector connects the relevés of subsequent years. The vectors are colour coded according to the direction of species compositional change. Red = directional change; dark red = change of ambiguous direction; green = semi-circular change; blue = circular change.

the years than in lowland habitats, where only the hemicryptophytes oscillated to a similar extent. In both habitats, life forms that oscillated strongly over the years in response to the seasonal rainfall ended at a lower cover rate in the drought year of 2017 than their starting position in 2001.

Discussion

Despite the wealth of in-depth studies, some of the research results regarding the processes that drive the vegeta-

tion dynamics in the arid rangelands are still ambiguous. Some long-term studies from the Succulent Karoo identified directional vegetation change that seemed to have followed biotic factors (Rahlao et al., 2008; van Rooyen et al., 2015). Other studies that analysed vegetation time series data from the arid summer rainfall region of South Africa and covered a period of 47 years (Masubelele et al., 2014) or 23 years (O'Connor & Roux, 1995) found that community change was driven primarily by external, abiotic factors such as rainfall variation.

Our study aimed to contribute another piece to the arid rangeland puzzle by analysing the vegetation dynamics of a rangeland in the Succulent Karoo over 17 years. Since the grazing intensity changed from high to low intensity at the time we commenced the monitoring activity, the generated time series vegetation data also describes the response of the vegetation to the release from heavy grazing pressure. We were therefore interested in how the vegetation responded and whether responses differed between upland and lowland habitats.

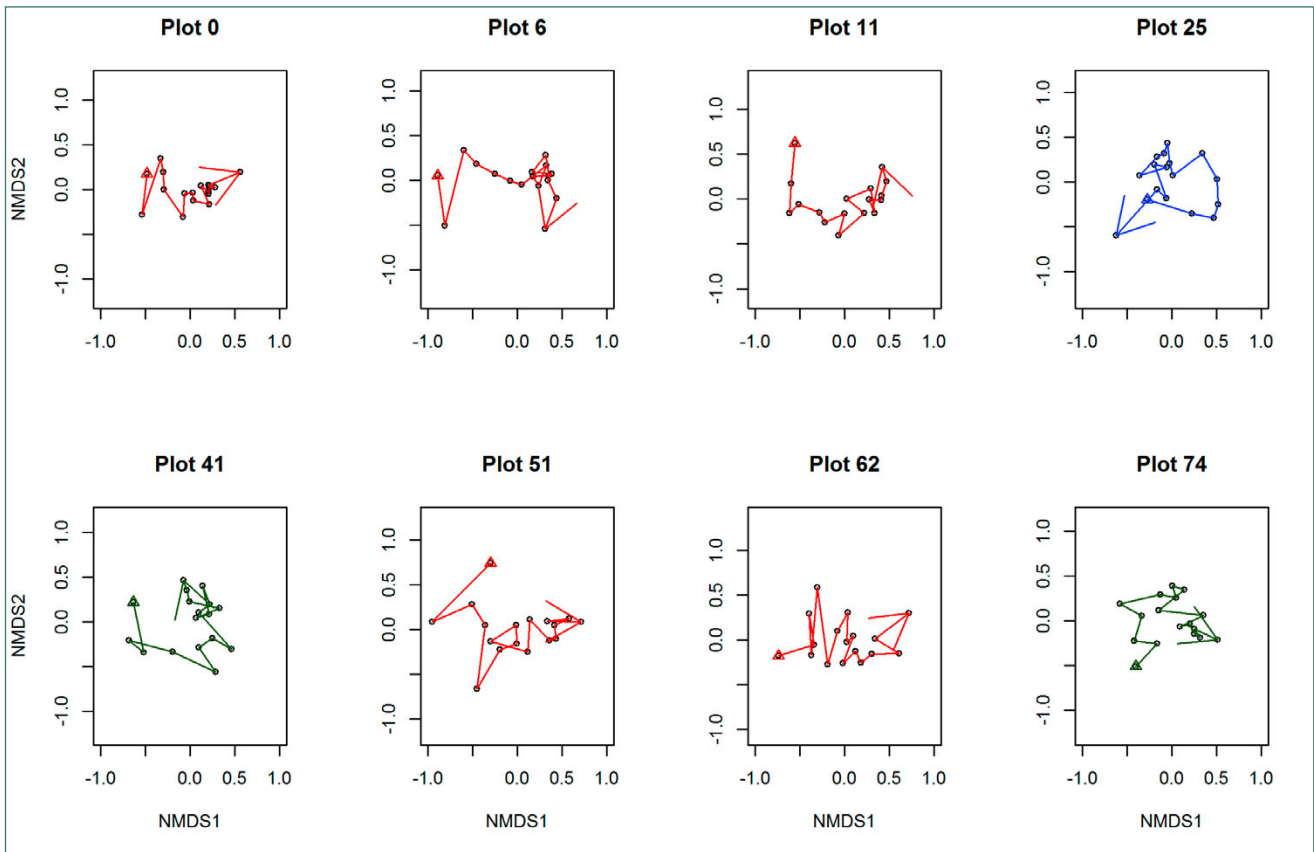


Figure 4: Non-metric multidimensional scaling (NMDS) ordination for the eight upland plots based on perennial species composition. Vectors connect relevés of subsequent years. The vectors are colour coded according to the direction of change in species composition. Red = directional change; green = semi-circular change; blue = circular change.

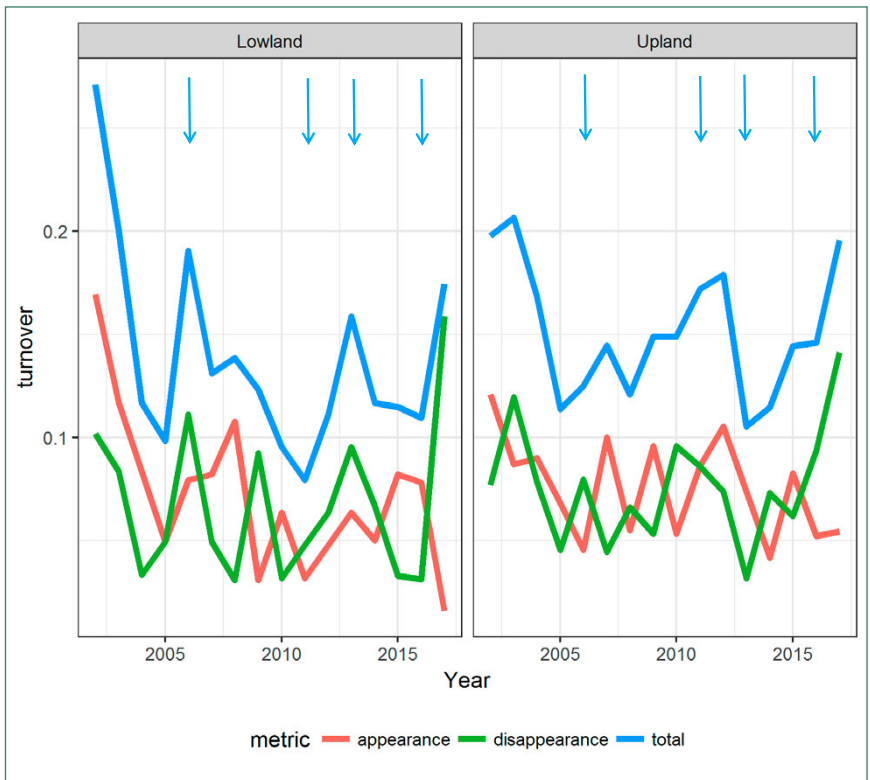


Figure 5: Species turnover based on the appearance and disappearance of perennial species per habitat type (lowland vs. upland) for the years 2001 to 2017. Red = appearance; green = disappearance; blue = total turnover (disappearance + appearance). Blue arrows indicate years with rainfall at 125% above the long-term average of 130 mm (see Fig. 1).

An overall ordination of the 17 relevés all the plots revealed a clear division of the vegetation resulting in 8 upland and 12 lowland plots based on the distinctly different species composition between the two habitat types. Also, the composition of perennial life forms differed, with a higher proportion of larger life forms in the uplands. The higher proportion of large shrubs at the upland habitats can be related to higher soil moisture in the run-on areas beneath the larger rocks and rock faces (Anderson et al., 2010). Upland habitats are also less accessible to livestock than the lowland habitats and are thus exposed to a lower grazing pressure for most of the year (Riginos & Hoffman, 2003; Petersen et al., 2004; Anderson & Hoffman, 2007). Vegetation studies from the Kamiesberg bioregion of Namaqualand, about 50 km inland from our study site, have showed that higher grazing pressure over several decades in the more homogenous lowlands can lead to sparser perennial vegetation cover and a higher proportion of opportunistic species such as therophytes and geophytes

as well as opportunistic chamaephytes with a shorter life span (Todd & Hoffman, 1999; Anderson & Hoffman, 2007). These opportunistic species can reach high cover values within a few good rainfall years but die back in a drought year. A higher proportion of opportunistic species among the perennials in the lowlands of our study explains the observed higher interannual fluctuation of appearing and disappearing species and of the total species turnover in lowlands compared to the uplands. The appearance and disappearance of species in a given plot depends on the seasonal rainfall. The fact that the appearances peaked with a time lag of one year are a result of seeds that germinate early in the growing season and are recorded as newly established individuals during the subsequent year after they have survived the dry summer.

We found that some life form types (e.g., Cnan and Cmac) responded to different extents to interannual rainfall variance in the two habitat types, suggesting that none of the life form types as defined here are generally more resilient to drought than others. Rather, the habitat-specific responses of the life forms result from the fact that the species that are dominant within a life form type differ between the two habitats and that species vary in ecological traits additional to those described by the life form type. Future analyses need to further refine the plant traits used, taking aspects such as life span and level of xeromorphy of the leaves as a general investment strategy to protect water against transpiration into consideration. The importance of a narrower differentiation of life form types has already been suggested by previous studies (Goldberg & Turner, 1986; Hoffman et al., 2009).

Lowland habitats had a higher species turnover rate than uplands, but this generally did not result in a directional change in vegetation. The single-plot ordinations for the lowland plots in most cases showed either circular or little change in the species composition over the 17 years. On the contrary, the relevés of most of the eight upland plots showed trajectories that can be interpreted as directional changes. These directional changes indicate that the upland habitats,

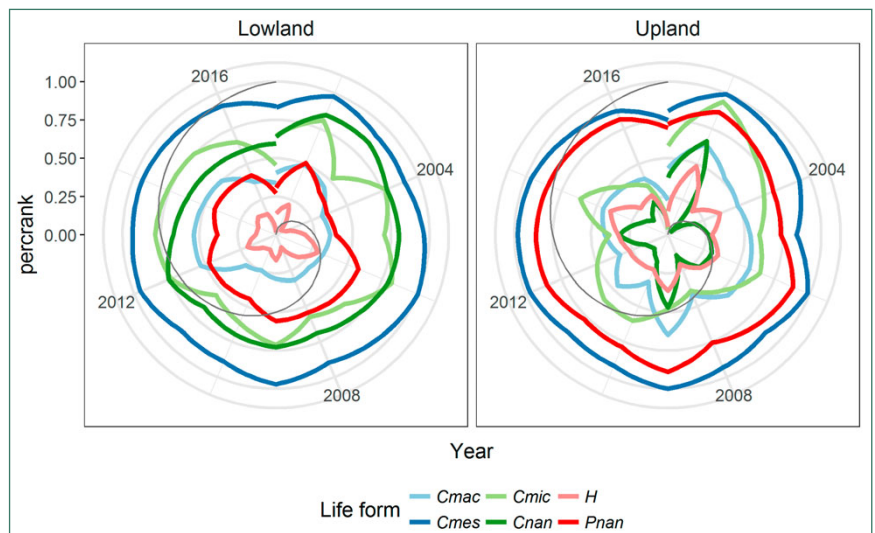


Figure 6: Cover rank clocks per habitat type (upland vs. lowland) for the vegetation classified into eight life-form types at Soebatsfontein: Cmac = macro-chamaephytes (30–50 cm height); Cmes = meso-chamaephytes (15–30 cm); Cmic = micro-chamaephytes (5–15 cm); Cnan = nano-chamaephytes (0–5 cm); H = hemicryptophytes; Pnan = nano-phanerophytes (50–100 cm).

which have been less impacted by grazing in the past, responded more quickly to the release of grazing pressure. Also the higher soil moisture content in the upland habitats (Anderson et al., 2010) may have facilitated a more rapid vegetation recovery. Lowland habitats that were more heavily impacted in the past reached a state that could not be changed without external interventions such as sowing or planting palatable species or introducing organic material into the degraded system (Milton et al., 1994; Simons & Allsopp, 2007). Only continuous monitoring will be able to show whether upland plots continue moving in one direction or merely describe larger circular patterns.

Beyond the general differences between upland and lowland habitats, the single plot ordinations also showed that each plot responded individually to the interannual variation in weather conditions. These differences can partly be explained by the high variance in species composition between the plots and by the species-specific responses to the interannual climatic variances and land use change. Also, the small-scale differences in soil features, which are typical for the Succulent Karoo (Petersen et al., 2010), and their effects on the water availability (Francis et al., 2007) add to the complexity of vegetation responses.

The few studies that continuously monitored the vegetation of South African drylands over a period long enough to disentangle the relative influences of climate and herbivory in these arid systems also revealed the complexity of the vegetation dynamics (O'Connor & Roux, 1995; Jürgens *et al.*, 1999; Kraaij & Milton, 2006; Schmiedel *et al.*, 2012; van Rooyen *et al.*, 2015; Vorster, 2017). All authors stress the importance of continuous long-term monitoring to obtain insight into the processes and their drivers. Additionally, O'Connor & Roux (1995), who analysed a vegetation time series of 23 years in the summer rainfall Karoo recorded at four-year intervals, concluded that if monitoring aims to detangle the contribution of internally driven and externally triggered recovery of rangelands, the monitoring interval needs to reflect the pace at which the vegetation of the study system changes, which in their case would have been annually. Also, our data suggest that an annual monitoring interval is critical to understand the vegetation dynamics. In our data, the heterogeneity in the direction and extent of change among the plots over the years would not have been detected if the monitoring had been conducted at longer intervals.

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References

- Anderson, P.M.L. & Hoffman, M.T. (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.
- Anderson, P.M.L., Hoffman, M.T. & O'Farrell, P.J. (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.
- Desmet, P.G. (2007) Namaqualand - A brief overview of the physical and floristic environment. *Journal of Arid Environments*, **70**, 570–587.
- Ellis, J.E. & Swift, D.M. (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Rangeland Ecology & Management/Journal of Range Management Archives*, **41**, 450–459.
- Francis, M.L., Fey, M.V., Prinsloo, H.P., Ellis, F., Mills, A.J. & Medinski, T.V. (2007) Soils of Namaqualand: compensations for aridity. *Journal of Arid Environments*, **70**, 588–603.
- Gillson, L. & Hoffman, M.T. (2007) ECOLOGY: rangeland ecology in a changing world. *Science*, **315**, 53–54.
- Goldberg, D.E. & Turner, R.M. (1986) Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology*, **67**, 695–712.
- Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J. et al. (2010) The BIOTA Observatories. *Biodiversity in southern Africa. Volume 1: Patterns at local scale — the BIOTA Observatories* (ed. by N. Jürgens, D.H. Haarmeyer, J. Luther-Mosebach, J. Dengler, M. Finckh, & U. Schmiedel), pp. 6–801. Klaus Hess Publishers, Göttingen & Windhoek.
- Hillmann, T., Mücke, G., Josenhans, K. & Jürgens, N. (2018) Online presentation of the SASSCAL ObservationNet. This volume.
- Hoffman, M.T., Carrick, P.J., Gillson, L. & West, A.G. (2009) Drought, climate change and vegetation response in the Succulent Karoo, South Africa. *South African Journal of Science*, **105**, 54–60.
- Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813.
- Jürgens, N., Gotzmann, I.H. & Cowling, R.M. (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.
- Jürgens, N., Schmiedel, U., Haarmeyer, D. et al. (2012) The BIOTA Biodiversity Observatories in Africa — a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment*, **184**, 655–678.
- Kraaij, T. & Milton, S.J. (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.
- Luther-Mosebach, J., Dengler, J., Schmiedel, U., Roewer, I.U., Labitzky, T. & Groengroeft, A. (2012) A first formal classification of the Hardeveld vegetation in Namaqualand, South Africa. *Applied Vegetation Science*, **15**, 401–431.
- Masubebele, M.L., Hoffman, M., Bond, W. & Gambiza, J. (2014) A 50-year study shows grass cover has increased in shrublands of semi-arid South Africa. *Journal of Arid Environments*, **104**, 43–51.
- Milton, S.J., Dean, W.R.J., du Plessis, M.A. & Siegfried, W.R. (1994) A conceptual model of arid rangeland degradation. *BioScience*, **44**, 70–76.
- Milton, S.J. & Hoffman, M.T. (1994) The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. *African Journal of Range and Forage Science*, **11**, 18–26.
- Mucina, L., Jürgens, N., Le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K.J., Powrie, L.W., Desmet, P.G. & Milton, S.J. (2006) Succulent Karoo biome. *The vegetation of South Africa, Lesotho and Swaziland* (ed. by L. Mucina and M.C. Rutherford), pp. 221–229. South African National Biodiversity Institute, Pretoria.
- O'Connor, T.G. & Roux, P.W. (1995) Vegetation changes (1947–1971) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology*, **29**, 247–260.
- Petersen, A. (2008) *Pedodiversity of southern African drylands*. University of Hamburg, Hamburg.
- Petersen, A., Groengroeft, A., Mills, A. & Mielich, G. (2010) Soils along the BIOTA transects. *Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale* (ed. by U. Schmiedel and N. Jürgens), pp. 84–92. Klaus Hess Publishers, Göttingen & Windhoek.
- Petersen, A., Young, E.M., Hoffman, M.T. & Musil, C.F. (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.
- Rahlao, S.J., Hoffman, M.T., Todd, S.W. & McGrath, K. (2008) Long-term vegetation change in the Succulent Karoo, South Africa following 67 years of rest from grazing. *Journal of Arid Environments*, **72**, 808–819.
- Raunkiaer, C. (1937) *Plant life forms*. The Clarendon Press, Oxford.
- Riginos, C. & Hoffman, M.T. (2003) Changes in population biology of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology*, **40**, 615–625.
- Schmiedel, U., Dengler, J. & Etzold, S. (2012) Vegetation dynamics of endemic-rich quartz fields in the Succulent Karoo, South Africa, in response to recent climatic trends. *Journal of Vegetation Science*, **23**, 292–303.
- Schmiedel, U., Linke, T., Christiaan, R.A. et al. (2010) Environmental and socio-economic patterns and processes in the Succulent Karoo frame conditions for the management of this biodiversity hotspot. *Biodiversity in southern Africa. Volume 3: Implications for land use and management* (ed. by M.T. Hoffman, U. Schmiedel, and N. Jürgens), pp. 109–150. Klaus Hess Publishers, Göttingen & Windhoek.
- Schmiedel, U., Röwer, I.U., Luther-Mosebach, J., Dengler, J., Oldeland, J. & Gröngroeft, A. (2016) Effect of grazing on vegetation and soil of the heuweltjieveld in the Succulent Karoo, South Africa. *Acta Oecologica*, **77**, 27–36.
- Simons, L. & Allsopp, N. (2007) Rehabilitation of rangelands in Paulshoek, Namaqualand: understanding vegetation change using biophysical manipulations. *Journal of Arid Environments*, **70**, 755–766.
- Todd, S.W. & Hoffman, M.T. (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, **142**, 169–178.
- van Rooyen, M.W., Le Roux, A., Geldenhuys, C., van Rooyen, N., Broodryk, N.L. & 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.
- Vetter, S. (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments*, **62**, 321–341.
- von Wehrden, H., Hanspach, J., Kaczynsky, P., Fischer, J. & Wesche, K. (2012) Global assessment of the non-equilibrium concept in rangelands. *Ecological Applications*, **22**, 393–399.
- Vorster, L. (2017) *Current status and impact (2004–2015) of indigenous ungulate herbivory on the vegetation of Sanbona Wildlife Reserve in the Little Karoo*. University of Cape Town, Cape Town.

References [CrossRef]

- Anderson, P.M.L. & Hoffman, M.T. (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. [CrossRef](#)
- Anderson, P.M.L., Hoffman, M.T. & O'Farrell, P.J. (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. [CrossRef](#)
- Desmet, P.G. (2007) Namaqualand - A brief overview of the physical and floristic environment. *Journal of Arid Environments*, **70**, 570–587. [CrossRef](#)
- Ellis, J.E. & Swift, D.M. (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Rangeland Ecology & Management/Journal of Range Management Archives*, **41**, 450–459. [CrossRef](#)
- Francis, M.L., Fey, M.V., Prinsloo, H.P., Ellis, F., Mills, A.J. & Medinski, T.V. (2007) Soils of Namaqualand: compensations for aridity. *Journal of Arid Environments*, **70**, 588–603. [CrossRef](#)
- Gillson, L. & Hoffman, M.T. (2007) ECOLOGY: rangeland ecology in a changing world. *Science*, **315**, 53–54. [CrossRef](#)
- Goldberg, D.E. & Turner, R.M. (1986) Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology*, **67**, 695–712. [CrossRef](#)
- Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J. et al. (2010) The BIOTA Observatories. *Biodiversity in southern Africa. Volume 1: Patterns at local scale — the BIOTA Observatories* (ed. by N. Jürgens, D.H. Haarmeyer, J. Luther-Mosebach, J. Dengler, M. Finckh, & U. Schmiedel), pp. 6–801. Klaus Hess Publishers, Göttingen & Windhoek.
- Hillmann, T., Muche, G., Josenhans, K. & Jürgens, N. (2018) Online presentation of the SASSCAL ObservationNet. This Volume. [CrossRef](#)
- Hoffman, M.T., Carrick, P.J., Gillson, L. & West, A.G. (2009) Drought, climate change and vegetation response in the Succulent Karoo, South Africa. *South African Journal of Science*, **105**, 54–60. [CrossRef](#)
- Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813. [CrossRef](#)
- Jürgens, N., Gotzmann, I.H. & Cowling, R.M. (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. [CrossRef](#)
- Jürgens, N., Schmiedel, U., Haarmeyer, D. et al. (2012) The BIOTA Biodiversity Observatories in Africa — a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment*, **184**, 655–678. [CrossRef](#)
- Kraaij, T. & Milton, S.J. (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. [CrossRef](#)
- Luther-Mosebach, J., Dengler, J., Schmiedel, U., Roewer, I.U., Labitzky, T. & Groengroeft, A. (2012) A first formal classification of the Hardeveld vegetation in Namaqualand, South Africa. *Applied Vegetation Science*, **15**, 401–431. [CrossRef](#)
- Masubelele, M.L., Hoffman, M., Bond, W. & Gambiza, J. (2014) A 50-year study shows grass cover has increased in shrublands of semi-arid South Africa. *Journal of Arid Environments*, **104**, 43–51. [CrossRef](#)
- Milton, S.J., Dean, W.R.J., du Plessis, M.A. & Siegfried, W.R. (1994) A conceptual model of arid rangeland degradation. *BioScience*, **44**, 70–76. [CrossRef](#)
- Milton, S.J. & Hoffman, M.T. (1994) The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. *African Journal of Range and Forage Science*, **11**, 18–26. [CrossRef](#)
- Mucina, L., Jürgens, N., Le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K.J., Powrie, L.W., Desmet, P.G. & Milton, S.J. (2006) Succulent Karoo biome. *The vegetation of South Africa, Lesotho and Swaziland* (ed. by L. Mucina and M.C. Rutherford), pp. 221–229. South African National Biodiversity Institute, Pretoria.
- O'Connor, T.G. & Roux, P.W. (1995) Vegetation changes (1947–1971) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology*, **29**, 247–260. [CrossRef](#)
- Petersen, A. (2008) *Pedodiversity of southern African drylands*. University of Hamburg, Hamburg.
- Petersen, A., Groengroeft, A., Mills, A. & Miehlich, G. (2010) Soils along the BIOTA transects. *Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale* (ed. by U. Schmiedel and N. Jürgens), pp. 84–92. Klaus Hess Publishers, Göttingen & Windhoek.
- Petersen, A., Young, E.M., Hoffman, M.T. & Musil, C.F. (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. [CrossRef](#)
- Rahlao, S.J., Hoffman, M.T., Todd, S.W. & McGrath, K. (2008) Long-term vegetation change in the Succulent Karoo, South Africa following 67 years of rest from grazing. *Journal of Arid Environments*, **72**, 808–819. [CrossRef](#)
- Raunkiaer, C. (1937) *Plant life forms*. The Clarendon Press, Oxford.
- Riginos, C. & Hoffman, M.T. (2003) Changes in population biology of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology*, **40**, 615–625. [CrossRef](#)
- Schmiedel, U., Dengler, J. & Etzold, S. (2012) Vegetation dynamics of endemic-rich quartz fields in the Succulent Karoo, South Africa, in response to recent climatic trends. *Journal of Vegetation Science*, **23**, 292–303. [CrossRef](#)
- Schmiedel, U., Linke, T., Christiaan, R.A. et al. (2010) Environmental and socio-economic patterns and processes in the Succulent Karoo frame conditions for the management of this biodiversity hotspot. *Biodiversity in southern Africa. Volume 3: Implications for landuse and management* (ed. by M.T. Hoffman, U. Schmiedel, and N. Jürgens), pp. 109–150. Klaus Hess Publishers, Göttingen & Windhoek.
- Schmiedel, U., Röwer, I.U., Luther-Mosebach, J., Dengler, J., Oldeland, J. & Gröngroft, A. (2016) Effect of grazing on vegetation and soil of the heuweltjieveld in the Succulent Karoo, South Africa. *Acta Oecologica*, **77**, 27–36. [CrossRef](#)
- Simons, L. & Allsopp, N. (2007) Rehabilitation of rangelands in Paulshoek, Namaqualand: understanding vegetation change using biophysical manipulations. *Journal of Arid Environments*, **70**, 755–766. [CrossRef](#)
- Todd, S.W. & Hoffman, M.T. (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, **142**, 169–178. [CrossRef](#)
- van Rooyen, M.W., Le Roux, A., Geldenhuys, C., van Rooyen, N., Broodryk, N.L. & 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. [CrossRef](#)
- Vetter, S. (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments*, **62**, 321–341. [CrossRef](#)
- von Wehrden, H., Hanspach, J., Kaczensky, P., Fischer, J. & Wesche, K. (2012) Global assessment of the non-equilibrium concept in rangelands. *Ecological Applications*, **22**, 393–399. [CrossRef](#)
- Vorster, L. (2017) *Current status and impact (2004–2015) of indigenous ungulate herbivory on the vegetation of Sanbona Wildlife Reserve in the Little Karoo*. University of Cape Town, Cape Town.