Journal of Vegetation Science **23** (2012) 292–303

Vegetation dynamics of endemic-rich quartz fields in the Succulent Karoo, South Africa, in response to recent climatic trends

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Keywords
Aizoaceae; Arid; Climate change; Diversity hotspot; Endemic; Global warming; Life form; Namaqualand; Precipitation; Species composition; Species richness; Succulent

Nomenclature
Germishuizen & Meyer (2003)

Received 30 October 2009
Accepted 4 August 2011
Co-ordinating Editor: Hans Henrik Bruun

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Abstract

Question: How do species composition and abundance change in the medium term and can the detected fluctuations and trends be attributed to weather conditions or climate change?

Location: Quartz fields of the Knersvlakte, Succulent Karoo, South Africa, a plant diversity hotspot.

Methods: We monitored vascular plant composition and abundance of all taxa on 12 permanent plots (25 m²) over a period of 12 yr. With multiple regressions, we tested the effect of rainfall in different periods on species richness and abundance.

Results: The plots showed significant inter-annual changes in population size, species richness and species composition. In general, plant populations showed a significant positive trend over the 12 yr analysed, while therophytes decreased significantly. Number of chamaephyte and geophyte individuals was positively influenced by rainfall of the preceding year, whereas therophytes were significantly positively influenced by rainfall of the same year.

Conclusions: We conclude that the increase in inter-annual variability of rainfall has so far had no negative effects on the quartz field vegetation. However, observations of recent climatic trends and climate change projections suggest that there will be much stronger changes in rainfall and temperature patterns in the next decades. Continuous long-term monitoring of biodiversity is thus crucial to understand potential impacts of climate change in the Knersvlakte.

Introduction

Current and future anthropogenic climate change is generally assumed to be one of the major threats to global biodiversity (Kappelle et al. 1999; Sala et al. 2000; McCarthy 2001; Thomas et al. 2004; Thuiller et al. 2005, 2008; Parmesan 2006). This is particularly true for regions that host many species of small geographical range and, at the same time, are predicted to experience severe climate change (Barnard & Thuiller 2008). Just such a case is Namaqualand, the arid winter rainfall area in western South Africa. Climate change scenarios for that area project increases in aridity and number of exceptional climate events (e.g. Hulme et al. 2001; Thomas et al. 2005; Christensen et al. 2007) and respective bioclimatic models based on climate change scenarios predict reduced species richness (Midgley et al. 2002; Midgley & Thuiller 2007).

However, the predictive power of such models is strongly dependent on empirical data based on in situ observations and experimental evidence (Araújo et al. 2005). While for other regions of the world there is sound and unequivocal evidence of the ecological impacts of recent climate change (Hughes 2000; Walther et al. 2002; Le Roux & McGeoch 2008; Parolo & Rossi 2008), for arid southern Africa the few empirical studies on climate change effects on vegetation (Milton et al. 1995; Jürgens et al. 1999; Midgley & van der Heyden 1999; Carrick 2001; Midgley & Thuiller 2007; Musil et al. 2009) are partly contradictory. On the one hand, Foden et al. (2007) found a decline of populations of the tree-like succulent *Aloe*

Doi: 10.1111/j.1654-1103.2011.01346.x

dichotoma with proximity to the equator, which they attributed to climate change, and Musil et al. (2009) found increased plant mortalities when they experimentally raised temperatures at sites in southern Namaqualand to levels predicted by climate scenarios. On the other hand, Jürgens et al. (1999) mostly found a steady state or even increase of species richness and abundance in the Richtersveld in northwestern Namaqualand from 1980 to 1996 following a severe drought in 1978–1979, which decimated plant populations in the area. A similarly positive trend in vegetation cover of leaf succulent shrubs has been revealed by Rahlao et al. (2008) in their analysis of vegetation change in the southern Succulent Karoo, which they related to 67 yr of resting from livestock grazing. During the same period, annual rainfall did not show any significant trend in the studied area.

The few available empirical studies on the response of succulent vegetation to climatic extremes (see Hoffman et al. 2009 for synthesis) suggest that drought tolerance varies among life forms, plant strategy types and stages of life. Seedlings of succulent shrubs, for instance, showed a significantly higher drought tolerance compared to non-succulent shrub seedlings (Esler & Philips 1994; Carrick 2001; Lechmere-Oertel & Cowling 2001). The drought tolerance of adult succulents, however, showed a more inconsistent pattern: adult succulent shrubs that experienced a long period (i.e. 137 or 232 d) without sufficient rainfall events (>5 mm) had a similar (Carrick 2001) or even better (Milton et al. 1995) survival rate than non-succulent shrubs. On the other hand, rain sheltering experiments revealed that succulent shrubs were less drought-tolerant than non-succulent species. Two of the four deeper rooting non-succulent shrubs survived the complete exclusion of rain for 600 d with little damage (Midgley & van der Heyden 1999). However, such uninterrupted droughts without even small amounts of water input do not occur under natural conditions in the Succulent Karoo. Midgley & van der Heyden (1999) showed that succulent shrubs with typically shallow roots are capable of responding rapidly to even small water inputs. These short phases of rehydration allow them to avoid mortality even under severe droughts. Life stage, as well as amount, interval and timing of rainfall seem to be critical for the survival of succulent and non-succulent shrubs under drought conditions. Also, the various life strategy types among southern African succulents influence the response of the populations to drought and rainfall events (Jürgens et al. 1999). This broad variety of responses of plant species to rainfall variation has been shown to strongly drive community changes in the southern African Karoo (O'Connor & Roux 1995; Hoffman et al. 2009).

Our study aims to contribute to the ongoing discussion by filling the critical gap of in situ measured, individual-based population monitoring data of succulent plant species in the southernmost part of Namaqualand, the Knersvlakte. The Knersvlakte is a centre of vascular plant species richness and endemism in the winter rainfall desert in western South Africa (Hilton-Taylor 1994). Typical of the Knersvlakte is the frequent island-like occurrence of an azonal habitat type, the quartz gravel fields (hereafter referred to as quartz fields). Quartz fields differ significantly from the surrounding areas in both soil properties and vegetation. They are dominated by dwarf succulent plants, mainly from the families Aizoaceae and Crassulaceae (Schmiedel & Jürgens 1999). Quartz field species are adapted to the specific microclimate (Schmiedel & Jürgens 2004) and to edaphic aridity caused by high salinity and shallowness of the soil (Schmiedel & Jürgens 1999). Corresponding to the small-scale mosaic of soil properties, the mostly monodominant vegetation units of quartz fields (Table S1) show high spatial turnover that leads to a high beta-diversity (Schmiedel & Jürgens 1999). About 40% of the 150 endemic vascular plants of the Knersvlakte are restricted to quartz fields (Schmiedel 2004).

For the Knersvlakte, the climate change models project a change (compared to 1961–1990) in mean annual temperature between +1.5 K (for a moderate scenario) and +8 K (for the most extreme scenario; Hulme et al. 2001). According to the GIS models of climatic variables of MacKellar et al. (2007) for the period 1950–1999, the Knersvlakte saw a less pronounced seasonality of precipitation, i.e. was drier during the normal rainy season in winter, but wetter in other seasons. Based on climatic data and a quantitative analysis of inter-annual population dynamics in permanent plots in the Knersvlakte over 12 yr, this study aims to answer the following research questions:

What are the trends and fluctuations in vegetation composition of the quartz fields and in populations of individual species under the current climate conditions?

How do fluctuations in vegetation composition and population dynamic of individual species relate to inter-annual rainfall patterns?

Based our findings, we discuss how the quartz field taxa may be affected by future climate change.

Methods

Study area

The Knersvlakte bioregion is situated in the winter rainfall-influenced Namaqualand-Namib Domain of the Succulent Karoo Region (in the sense of Jürgens 1991) in the northwest of South Africa (Fig. 1). It comprises approximately 10 000 km^2 of a gently undulating plain, bound in the south and east by the Hantam and Bokkeveld, to the north by the Hardeveld, and to the west by the Namaqua-

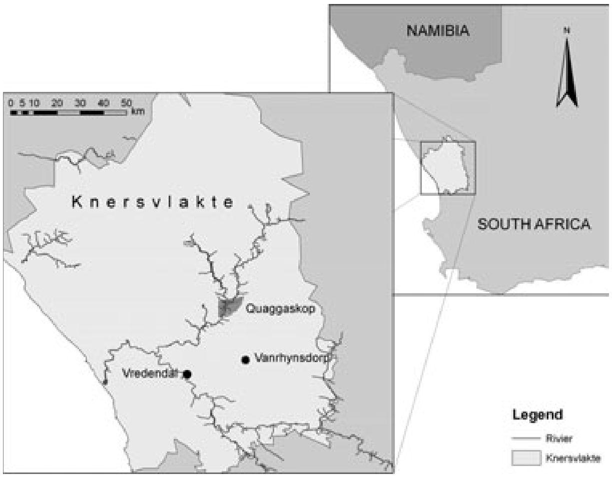

Fig. 1. Location of the study site Quaggaskop in the Knersvlakte in South Africa.

land Sandveld bioregion (Desmet 2007). The Knersvlakte is underlain by heterogeneous sediments of the Nama Group, dominated by shale, phyllite and limestone, and is intruded by numerous quartz veins (Watkeys 1999) from which the gravel layer of the quartz fields originates (Schmiedel & Jürgens 1999).

In comparison to other arid areas in southern Africa, Namaqualand in general is characterized by mild climate conditions and highly predictable winter rainfall (Desmet 2007). The Knersvlakte receives an average annual rainfall of 150 mm, with the wet season ranging from May to September. Advective fog, as well as the occurrence of dew, has great importance as a supplementary water resource for plant growth (Desmet 2007). Mean annual temperature in the Knersvlakte ranges from 17.9 to 18.6 °C, and on average three to five frost days occur per year (Mucina et al. 2007).

The study was carried out on the farm Quaggaskop (31° 24′S, 18°38′E, 140 m a.s.l.) in the central Knersvlakte (Fig. 1). This farm belongs to the unit SKk3 (Knersvlakte Quartz Vygieveld) of the classification of natural vegetation of South Africa (Mucina et al. 2007). Quaggaskop is dominated by quartz fields (Fig. 2) and has not been grazed by domestic livestock for more than 40 yr, so that the quartz fields here can be regarded as nearly undisturbed by direct human impact (Haarmeyer et al. 2010b). The soils of the quartz fields are up to 30 cm deep, vary widely in pH, salinity (Table S1) and stone content, and are rich in silt (Schmiedel 2002).

Climate data

Climate data were obtained from the Weather Bureau in South Africa for Vanrhynsdorp (25 km south of the study area) and Vredendal (30 km southwest of the study area; see also Fig. 1). The closer weather station positioned at Vanrhynsdorp belongs to the same weather system and thus experiences the same conditions as the study site regarding intra- and inter-annual rainfall variability but received higher total annual rainfall than the latter (i.e. 152 mm compared to ca. 125 mm at the study site). The difference in total annual rainfall is due to a south-north rainfall gradient in the Knersvlakte (compare also climate data of the Ratelgat Observatory, situated 15 km north of our study site, in Haarmeyer et al. 2010a).

The weather recordings included some unreliable monthly values due to missing daily values and some completely missing monthly values. Since only 1% of data were affected, we followed the suggestion of Harrell

Fig. 2. Patches of quartz fields in the Knersvlakte, South Africa. Insert: *Oophytum nanum* (Aizoaceae), a quartz field endemic of the Knersvlakte (photographs: S. Etzold).

Doi: 10.1111/j.1654-1103.2011.01346.x

(2001) to impute the missing data. The data marked in the source as 'unreliable' were simply retained, while missing data were replaced by means of the respective value in the preceding and subsequent month of the same year and of the same month in the two 'adjacent' years. We used these 'corrected' monthly data to calculate the annual rainfall.

Recording of vegetation composition and plant populations

In 1993, we established seven permanent plots (5 m × 5 m), and in 1995 we added one further such plot. The plots were selected to represent the major vegetation types on quartz fields of the Knersvlakte (Fig. 1) and were placed in areas with visually homogeneous vegetation and soil.

Generally, we counted the individuals of all vascular plants in Aug to Oct 1993, 1996, 1998, 1999, 2000 and 2005, in Apr 1995 and in Jul 1997. However, no abundance data were recorded for plot no. 4677 in 1993, no. 3019 in 1997 and no. 2877 in 1999. From the perennial species, only those that had survived at least one dry season were considered, and the often numerous seedlings from the year of observation were disregarded. In a few cases where a species occurred in extremely high numbers in a plot, only coverage and not abundance was recorded, or abundance in 25 m^2 was estimated by counting the number of individuals on a representative subplot of 1 m^2. Unidentified species were collected as herbarium specimens (see Table S2) and counted as separate taxa in all analyses.

Statistical analyses of vegetation data

For 52 species × plot × year combinations (4.1%) no abundance data were available for several reasons (see section Climate data), so we imputed the missing values based on the rest of the matrix following the suggestion of Harrell (2001). Missing values of species that occurred in more than one plot ($n = 48$) were imputed as follows: (1) we calculated relative abundance of this species in the respective year compared to the average abundance in the remaining years for all other plots with this species and averaged this value among these plots ($= x$); (2) we calculated the average abundance of this species in the respective plot for all other years except the missing one ($= y$); and (3) we estimated the abundance of the species in the respective year and plot as $x \cdot y$. Missing values of species that occurred in a single plot ($n = 6$) were imputed as means of the previous and the following recording. When the imputed 'abundances' were below 0.5 ($n = 3$), the species was regarded as absent from the plot in the respective year.

In the analyses, we considered the following dependent variables per plot and year: species richness (S), relative species richness (i.e. richness in the respective year divided by the mean richness over all years studied), relative abundance of a species (i.e., abundance N in the respective year divided by the mean abundance over all years studied), abundance sum (i.e. total number of individual plants), Shannon index ($H' = -\Sigma\, p_i \cdot \ln p_i$) and evenness ($E = H'/H_{max}$), with i indexing the species and p_i being the abundance of species i divided by the abundance sum. Further, we considered the following 'change variables': relative annual (re-) establishments ($= S_{re}/S_{Yr-1}$), extinctions ($= S_{ext}/S_{Yr-1}$) and net change of species composition ($= [S_{Yr} - S_{Yr-1}]/S_{Yr-1}$), as well as annual rate of increase in the population size of species ($\lambda_i = N_{i,Yar}/N_{i,Yar-1}$; cf. Silvertown & Charlesworth 2001), with S being the number of species in a plot and $N_{i,Year}$ the abundance of species i in a particular year. When periods between two subsequent recordings were longer than 1 yr, we assumed constant rates of the 'change variables' for the whole period. For inferential statistical analyses (regressions and ANOVAs) we used the dependent variables untransformed (cf. Wilson 2007), unless they deviated strongly from normal distribution or variance homogeneity. In the latter case, which was true for relative abundance of species, abundance sum, and year-to-year λ, we used $\log_{10}$-transformed values of the dependent variables in order to better meet the requirements of the applied statistical tests (cf. Quinn & Keough 2002). For the application of log transformation, relative abundance had to be related to the geometric instead of the arithmetic long-term mean.

Since year-to-year λ and the logarithm of relative abundance are not defined for abundance values of zero in any of the studied years, we had to replace zeros by an arbitrary small value for these calculations (cf. the suggestions of Quinn & Keough 2002; for log transformations). We used 0.25 as replacement, arguing that the abundance values in the sampled permanent plots can be regarded as integer estimates of population means of all stands of the respective vegetation type in the respective year. While, for example, an integer of the mean abundance of 1 denotes that the actual mean lies somewhere between 0.5 and 1.5; an integer of the mean abundance of 0 denotes that the actual mean lies between 0.0 and 0.5. Thus, it is reasonable to use the mean of the latter range (0.25) as replacement in the respective calculations. Moreover, this approach avoids the strong bias of results that is caused by the complete exclusion from the analysis of populations that have gone extinct (or have newly established) during the study period, as is applied in some comparable studies (e.g. Matthies et al. 2004).

In arid areas like the Succulent Karoo, establishment of new individuals is often restricted to above average rainfall years, whereas drought years may result in an increase of diebacks (Ihlenfeldt 1994; Jürgens et al. 1999). To test whether relative abundance per species and life form as well as species abundance in specific years can be explained by the rainfall regime, we applied multiple linear regressions with log-transformed relative abundance as the dependent variable and the rainfall of the closest weather station (Vanrhynsdorp) of the present plus the four preceding years as predictors.

The statistical analyses of vegetation data were carried out with Excel 2003 (Microsoft, Redmond, WA, USA) and STATISTICA for Windows (Version 7.1; StatSoft, Inc., Tulsa, OK, USA).

Results

Climate

The two weather stations showed congruent fluctuations in annual rainfall, and both gave a long-term average annual rainfall of 152 mm (Fig. S1). During the study period, the years 1993, 1995–1997 and 2001–2002 received rainfall above average, while below-average rainfall was recorded in the years 1994, 1998–2000 as well as 2003–2005. The wettest years were 1996 (mean rainfall for the two stations: 270 mm) and 1993 (250 mm), while 2003 (85 mm) and 2005 (92 mm) were driest.

Vegetation composition and plant populations

In the eight plots (each 25 m²), we recorded a total of 67 vascular plant terminal taxa (Table S2) during the 12-yr study period. Sixteen species occurred in at least half of the plots, and only one (*Tylecodon pygmaeus*) was found throughout (Table S2). Nearly all taxa were more or less succulent, and in terms of species numbers, chamaephytes ($n = 51$) dominated, while therophytes ($n = 10$) and geophytes ($n = 6$) played a subordinate role (Table S2). Among plant families, Aizoaceae (31 species) and Crassulaceae (10 species) prevailed.

Per-year vascular plant species richness per plot ranged from four to 38 taxa (mean = 13.2 ± 8.4 SD; for long-term means per plot, see Table S1), while cumulative species richness over 12 yr ranged from eight to 47 taxa (mean = 20.0 ± 12.5 SD). Total number of plant individuals (abundance sum) per 25 m² varied considerably between plots and years, with a minimum of 49 and a maximum of ca. 13 000 plants (mean: 1 560 ± 2 590 SD). The highest individual abundances (>200 and up to several thousand per plot) were reached by the five succulent Aizoaceae species, *Argyroderma delaetii*, *A. fissum*, *A. pearsonii*, *Mesembryanthemum fastigiatum* and *Oophytum nanum*. Abundance-based evenness (temporal means) showed pronounced idiosyncrasies for the different plots, with values from 0.06 to 0.67 (mean: 0.45 ± 0.19 SD), while the inter-annual variability of 0.08 ± 0.04 SD was less pronounced.

Both log-transformed abundance sum ($P = 0.002$) and species richness ($P < 0.001$; Fig. 3) showed a significant general pattern of inter-annual changes. Log-transformed abundance sum significantly (at $\alpha = 0.05$) exceeded long-term average in the years 1997 and 2005, while it declined significantly in 1993 and 1995. Species richness was significantly above average in 1996 and 1997 and below average in 1999 (Fig. 3).

The relative changes in species composition between consecutive years followed distinct patterns (Fig. 4). The differences between years were highly significant for local (i.e. plot-wise) extinctions ($P < 0.001$), local (re-)establishments ($P < 0.001$) and net change in species richness ($P = 0.004$). By contrast, none of the three parameters of relative compositional change differed significantly between plots. In particular, annual extinction rates from 1997 to 1998 were significantly higher than for any other period studied (at $\alpha = 0.05$). The pronounced extinction rate was mainly due to a decrease in abundance of therophytes and geophytes, which showed a much stronger response than chamaephytes (Fig. 5).

When analysing population sizes (expressed as log-transformed relative abundances) in the complete data set (i.e. 160 species–plot combinations for 8 yr), a clear pattern emerged ($P < 0.001$), with population sizes being high in 1996, 1997 and 2005, but low in the other years

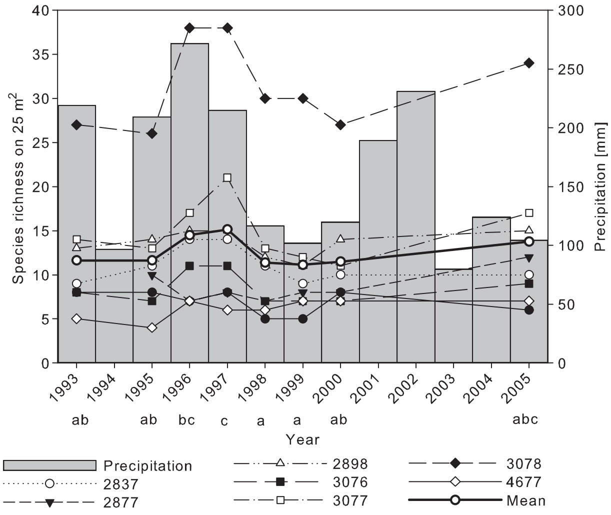

Fig. 3. Inter-annual changes of vascular plant species richness on the eight 25-m² permanent plots and mean value across the sites. Numbers in legend refer to the identification numbers of the long-term monitoring plots. Columns show total annual precipitation (Vanrhynsdorp weather station). Lowercase letters indicate homogeneous groups of years for residuals of plant species richness according to Tukey's HSD post-hoc test, applied to the ANOVA results.

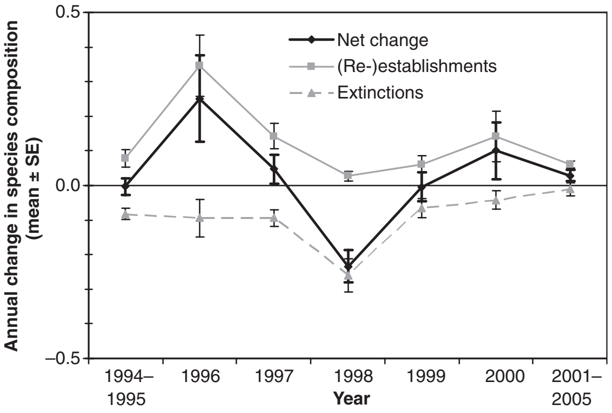

Fig. 4. Relative annual changes in species composition, shown as mean value for the eight permanent plots of 25 m². The net change in species richness is partitioned into gains (plot-wise re-establishments) and losses (i.e. plot-wise extinctions).

(Tukey's HSD at $\alpha = 0.05$). Looking at the three major life forms separately, they all showed a strong interaction with year. In general, the inter-annual fluctuations in population size increased from chamaephytes through geophytes to therophytes (Fig. 5). We also found highly significant interactions between plot and year ($F_{49,1216} = 2.9882$; $P < 0.001$). ANOVAs for the log-transformed population growth parameter λ yielded similar significant results as for log-transformed relative abundances, both for stand-alone effects of year and for interactions with plot (not shown). However, the differentiation between years was even more pronounced (Fig. 6).

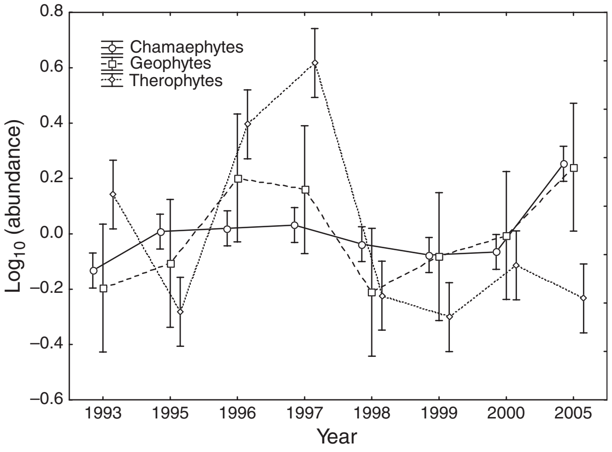

Fig. 5. Results of a two-way ANOVA of log-transformed relative abundance dependent on year and life form. The effects of year ($F_{71\ 216} = 12.201$) and year × life form ($F_{14\ 1256} = 13.949$) were both highly significant ($P < 0.001$), while life form alone had no effect due to the definition of relative abundances (they equal zero for each species).

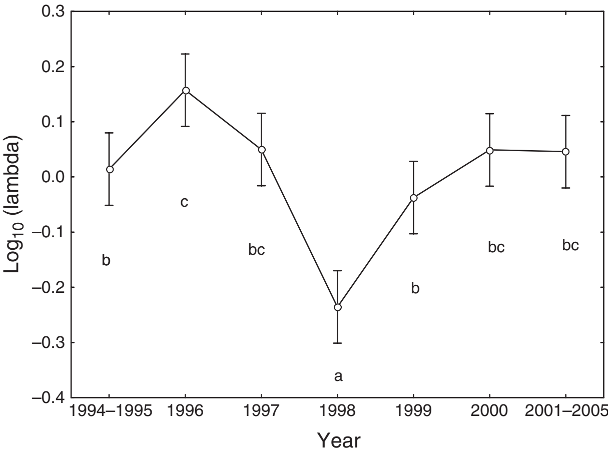

Fig. 6. Results of a one-way ANOVA of the log-transformed population growth parameter λ dependent on year ($F_{6,1\ 113} = 12.201$; $P < 0.001$). Homogeneous groups according to Tukey's HSD test (at $\alpha = 0.05$) are indicated with lower-case letters. Bars indicate 95% confidence intervals.

Linear regression of log-transformed relative abundance against year for the whole data set yielded a highly significant positive long-term trend, although it explained a relatively small proportion of the overall variability (Table 1). Separate analyses of the three life forms resulted in stronger trends, which were positive for chamaephytes and geophytes, but negative for therophytes (Table 1). The picture remained essentially the same when looking at individual species (Table S2). Of the 11 chamaephyte species with significant regressions, ten showed a positive trend, with *Malephora purpureo-crocea* being the only exception (Table S2). Similarly, among the geophytes, the two significant regressions were positive, while all ten therophyte species showed a decreasing 12-yr trend (Table S2). For the 12-yr period, the mean population growth parameter λ of the species studied ranged from 0.79 to 1.35, with mean values of 1.05 (±0.10 SD) for chamaephytes, 1.04 (±0.09 SD) for geophytes and 0.93 (±0.06 SD) for therophytes (Table S2). Different plant species showed contrasting population dynamics (i.e. inter-annual fluctuations and long-term trends). Figure S2 shows the popula-

Table 1. Results of the linear regression analysis of log-transformed relative abundance against year for all taxa and for life form separately (n = number of species–plot combinations; b_1 = slope of the regression function).

	n	b_1 [a^{-1}]	R^2	P
All Species	160	+0.012	0.010	< 0.001
Chamaephytes	120	+0.023	0.057	< 0.001
Geophytes	9	+0.025	0.060	0.038
Therophytes	31	–0.037	0.046	< 0.001

tion dynamics of eight important taxa of the quartz field flora in the Knersvlakte.

Climate–plant interactions

Rainfall regime of the recent and the four previous years explained part of the variation in species abundances (Table 2). The regression models for the four plant groups (all vascular plants combined, chamaephytes, geophytes, therophytes) were all significant. However, the explained variance was generally low, and only somewhat higher for therophytes (Table 2). While the rainfall in the year prior to recording had a strong and significant positive influence on the abundance of all plant groups, the rainfall in the year of recording increased the number of therophyte individuals but reduced the numbers of the other taxa (Table 2).

Discussion

Vegetation composition and plant populations

The spatial variability in species richness, evenness and individual abundance is characteristic of the small-scale soil and vegetation patterns of the quartz field mosaics in the Knersvlakte (Schmiedel & Jürgens 1999; Ellis & Weis 2006). The strong spatial variation in abundance sum between the plots is due to the occurrence of minute plant species (e.g. *Oophytum nanum*, *Argyroderma* spp.) in some of the plots, which are typical of quartz fields and can reach very high densities (cf. plot 2898) (Schmiedel & Jürgens 1999).

Response of plant populations to extreme years

Above-average rainfall years resulted in a significant increase in the number of therophytes in the same year and of newly established (i.e. 1-yr-old) chamaephyte individuals in the subsequent year. Expectedly, the occurrences of therophytes strongly increased the number of species per plot.

The dynamics of abundances in populations during the study period may be more indicative for the long-term trends of the vegetation than the variance in species richness. Extreme events like the unusually wet year 1996 and the drought period 1998–1999 caused significant variance in abundances. The exceptionally strong effect of the 1998 drought, which had the most severe effect on population densities (mainly geophytes and therophytes), is particularly remarkable since 1998 was not the year with the lowest annual rainfall in the study period. The very negative trend of the plant populations in 1998 can be attributed to the inter-annual rainfall pattern that resulted in relatively high rainfall in May (i.e. 44 and 51 mm at the two stations), which was not followed up by sufficient rainfall during the subsequent months, thus resulting in low abundance of therophytes and geophytes. This supports the results from other studies that showed that in addition to the total annual rainfall, other meteorological variables like the seasonal timing of rainfall (Brown 2002; Lucas et al. 2008) or the efficiency of the single rainfall events (Carrick 2003; Robinson 2004) can have an effect on population dynamics in arid biomes.

Several studies have shown a strong influence of climate on the dynamics of various ecosystems (for review see McCarthy 2001). This is particularly true for deserts (Goldberg & Turner 1986; Turner 1990; Bowers et al. 1995; Cody 2000) and has also been shown for the Succulent Karoo (Yeaton & Esler 1990; von Willert et al. 1992; Milton et al. 1999; Hoffman et al. 2009). Episodic germination events as a response to favourable rainfall have been confirmed by other studies on quartz-field plant populations (Stopp 1954). It has also been shown for the long-lived tree aloe, *A. pillansii* (Duncan et al. 2006). Ihlenfeldt (1994) emphasized that long-term climatic cycles may cause a complete or nearly complete breakdown of populations in the Succulent Karoo, which has also been observed by Jürgens et al. (1999). Our data show that even dwarf shrub populations on quartz fields, like *Argyroderma* spp. and *Conophytum* spp., which are known for having a comparatively long life span of up to 35 and even more than 130 yr, respectively (Stopp 1954), showed a measurable response

Table 2. Overview of the linear regression models for log-transformed relative abundance of species vs rainfall regime of the same year and four previous years for all vascular plants combined and for the three life forms separately. In the second column, the number of data points (*n*) used for the regression is given, followed by the goodness-of-fit parameters of the whole model. In the five columns to the right, standardized beta coefficients of the model parameters are listed with their significance level (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

				Annual Rainfall				
	n	R^2adj.	*P*	Year – 4	Year – 3	Year – 2	Year – 1	Year
All Species	1280	0.068	< 0.001	–0.03	–0.16***	–0.20***	+0.20***	–0.06
Chamaephytes	960	0.105	< 0.001	–0.15***	–0.29***	–0.26***	+0.14***	–0.30***
Geophytes	72	0.148	0.008	+0.05	–0.11	–0.41**	+0.31*	–0.06
Therophytes	248	0.250	< 0.001	+0.22*	+0.09	–0.06	+0.31***	+0.46***

Doi: 10.1111/j.1654-1103.2011.01346.x

to drought and high rainfall years. However, in accordance with Jürgens et al. (1999), our results showed different degrees of species' drought resistance, corresponding to life form. Expectedly, chamaephytes responded less strongly to rainfall than geophytes and therophytes. The different responses among succulent plants may also reflect the broad range of flexible C3/CAM (crassulacean acid metabolism) photosynthesis strategies that have been studied for only a few of the species so far (von Willert et al. 1990, 1992; Herppich & Herppich 1997; Veste et al. 2001). Our analysis of the direct interaction between annual rainfall and abundance also showed that total annual rainfall explained only part of the dynamics in populations, indicating that other parameters, like the temporal distribution and amount of single rainfall events, may be critical as well.

Long-term trend in vegetation

The perennial plant populations of the specialized and locally endemic quartz field vegetation in the Knersvlakte showed an overall positive trend over the last 12 yr of observation. This is particularly remarkable since the weather station in Vanrhynsdorp showed significant changes of the inter-annual variability of total annual rainfall from 1922 until 2005, with the 5-yr standard deviation having increased by a mean annual rate of 0.48 mm (U. Schmiedel, J. Dengler, S. Etzold unpublished data, see also Fig. S1). This past trend resulted in years with a total annual rainfall of <30% of the long-term average during the study period. During the recent past (1959–2005), also annual mean temperature and annual maximum temperature showed a significant positive trend (Schmiedel et al. unpublished data): regressions indicate that these two parameters have increased by 1.2 and 1.8 K, respectively, during the 46 yr. By contrast, annual minimum temperature and annual temperature amplitude showed no significant linear trend.

Only the therophytes showed a significantly negative trend during the 12 yr of observation. This result can be attributed to the two last years of observation (2000, 2005) which had exceptionally low rainfall. The same is true for the overall negative trend of the rather opportunistic chamaephyte species *Malephora purpureo-crocea*, which dies back during drought years.

Our observations of an overall positive trend in plant populations are supported by the similarly positive trends in species richness of annual and perennial plants that emerged from vegetation monitoring between 2001 and 2009 on 40 plots of 1000 m² in size elsewhere in the Knersvlakte (Vascular plants Sections for the Observatories S26–S28 in Haarmeyer et al. 2010a; Schmiedel et al. 2010). The overall positive trend in the quartz field populations may suggest that the near-endemic and habitat-specialized plant species, which are generally perceived as particularly vulnerable to the effects of climate change (Midgley et al. 2002; Travis 2003; Midgley & Thuiller 2007), are better buffered against variance in annual rainfall than previously thought.

One reason for this might be that the frequency and amount of fog and dew, which form an important additional source of moisture for plants in the Succulent Karoo (Desmet & Cowling 1999), might alleviate inter-annual rainfall variability in the study area. Even small amounts of this occult precipitation can measurably rehydrate the plants (Midgley & van der Heyden 1999; Martin & von Willert 2000). A recent study on the ecological importance of fog and dew in relation to rainfall for succulent plants in the study area revealed that the amount of fog and dew during the wet season (i.e. 158 mm) exceeds the amount of rainfall during the same period (138 mm) (I. Matimati, C. Musil, L. Raitt, E. February unpublished data). The same authors showed that fog and dew contribute significantly to the water supply of the plants during the wet season and may play an important role in alleviating water stress during the dry season. Another alleviating effect could possibly be attributed to the elevated atmospheric CO_2, which has been demonstrated to increase soil moisture, enhance plant water relations (Nelson et al. 2004) and favour the growth of woody species (Morgan et al. 2007).

Despite the overall positive trend in populations on the quartz fields of the Knersvlakte, conclusions regarding long-term trends under future climate change conditions have to be considered with great caution. Results from recent passive warming experiments in the Knersvlakte indicate that the quartz field species are currently growing close to their thermal tolerance limits. Even if the annual total rainfall and the occult precipitation of fog and dew would not change significantly, future temperature increase may have a fatal effect on these populations (Musil et al. 2009; Musil et al. 2010). We therefore have to assume that although the plant populations are coping with current climatic conditions, a warming climate will nevertheless increase evapotranspiration. This will, in turn, exert water stress on the plants, even if annual rainfall totals did not change significantly in the study area.

Our study revealed a strong response of plant populations, particularly of more opportunistic life forms (therophytes, geophytes, short-lived chamaephytes) to inter-annual rainfall variability. Our results suggest that the trends of increased inter-annual variability of rainfall and the increase of annual mean and annual maximum temperature that had been observed over the last decades in the study area did not have a negative effect on species richness during the study period. However, scenarios for future climate change project even stronger changes in temperature and rainfall patterns in the next decades.

Continued long-term monitoring of biodiversity and experimental approaches are required to fully understand the extent of the potential impacts of these climate changes in the Succulent Karoo.

Acknowledgements

The monitoring was set up and mostly done by U.S., except for the 2005 yr when S.E. carried it out. J.D. is responsible for the statistical analyses and drafted most of the Methods and Results sections, while U.S. and S.E. wrote the rest of the paper. All authors critically revised the whole manuscript. We would like to acknowledge Buys Wiese, on whose farm our research was carried out, the Cape Nature Conservation Board for issuing permits, and the Merensky Stiftung, Germany, for financial support. The project has been supported by the interdisciplinary biodiversity research and monitoring project BIOTA southern Africa, which was sponsored by the German Federal Ministry of Education and Research (BMBF) under promotion numbers 01 LC 0024, 01 LC 0024A and 01 LC 0024A2. Thanks to Jona Luther-Mosebach, Alexander Moßbrucker and Gerda Kriel for their help in the field, to Jan Möller and Jona Luther-Mosebach for assistance with the graphics, and to Daniela Haarmeyer and Britta Bösing for producing the map. The long-term weather data for Vanrhynsdorp and Vredendal were kindly provided by the Weather Bureau of South Africa. Finally, we are grateful to colleagues of the two vegetation ecology groups at the University of Hamburg, whose suggestions on earlier versions of the manuscript contributed to its quality. Timm Hoffman and four anonymous reviewers gave valuable comments on earlier versions of the manuscript. Curtis Björk polished our English usage.

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Doi: 10.1111/j.1654-1103.2011.01346.x

Supporting Information

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

Figure S1. Long-term development of annual rainfall for two weather stations in the Knersvlakte, namely Vanrhynsdorp (1922–2005) and Vredendal (1959–2005).

Figure S2. Contrasting population dynamics (i.e. inter-annual fluctuations and long-term trends) of eight typical vascular plants.

Table S1. Overview of basic data of the eight permanent plots studied.

Table S2. List of all vascular plant taxa found on the permanent plots with results of linear regressions of $\log_{10}$ (relative abundance) on year of record.

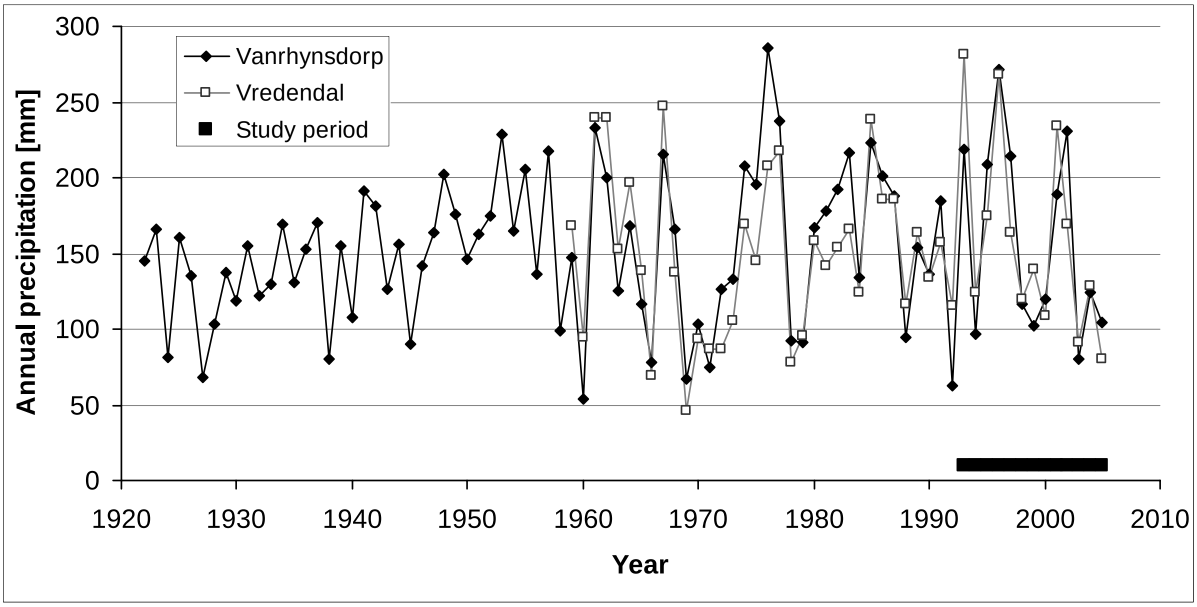

Fig. S1. Long-term development of annual rainfall for two weather stations in the Knersvlakte, namely Vanrhynsdorp (1922–2005) and Vredendal (1959–2005). Source: South African Weather Service.

The weather recordings included some unreliable monthly values due to missing daily values and some completely missing monthly values. Since only 1% of data were affected, we followed the suggestion of Harrell (2001) to impute the missing data. The data marked in the source as 'unreliable' were simply retained, while missing data were replaced by means of the respective value in the preceding and subsequent month of the same year and of the same month in the two 'adjacent' years. We used these 'corrected' monthly data to calculate the annual rainfall (Schmiedel et al. unpublished data).

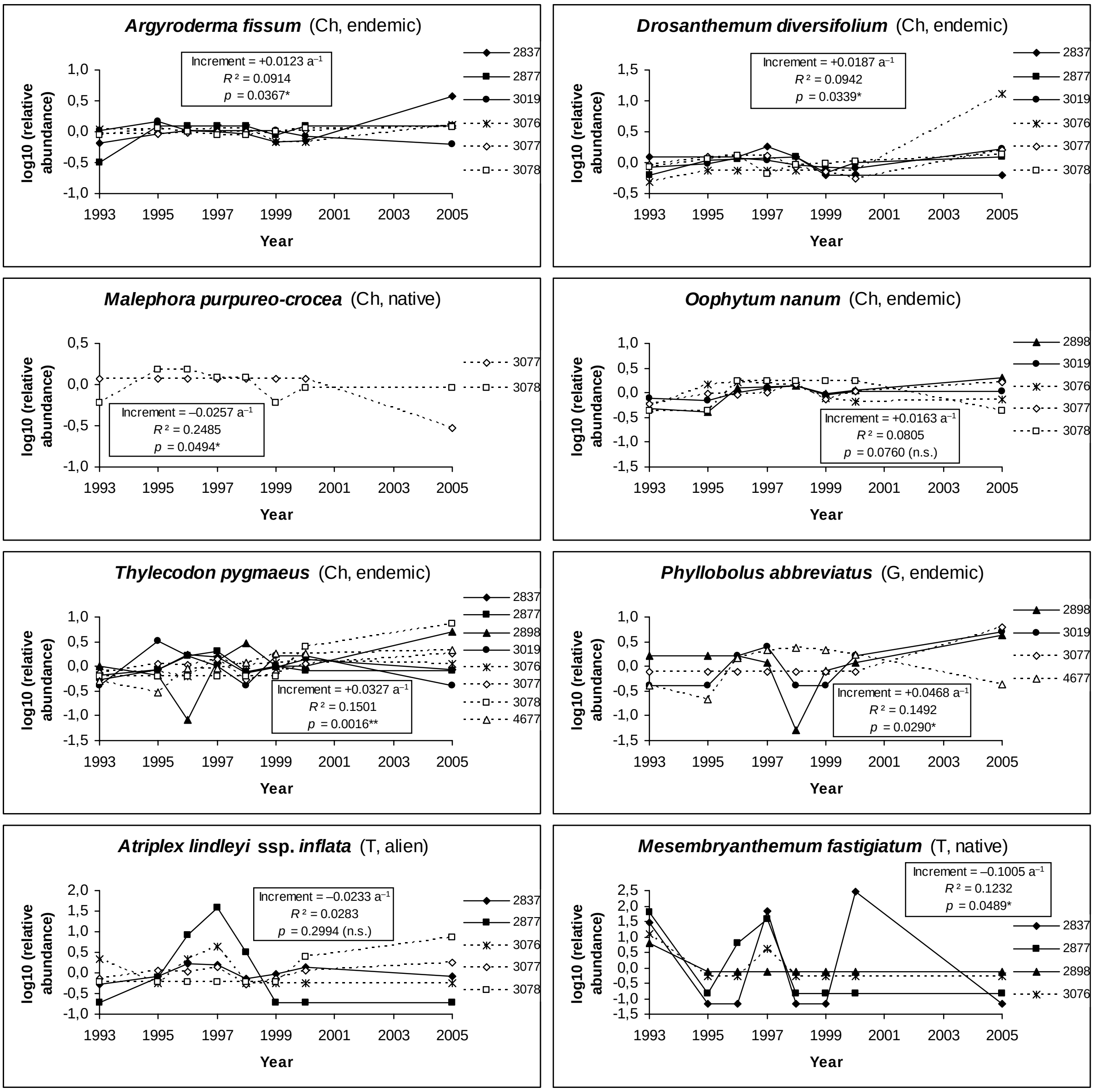

Fig. S2. Contrasting population dynamics (i.e. inter-annual fluctuations and long-term trends) of eight typical vascular plants of the quartz fields in the Knersvlakte. In each graph, the parameters of a linear regression of log-transformed relative abundance against year are displayed. Note that the scaling of the *y*-axis differs among the graphs. The numbers in the legends refer to the identification number of the long-term monitoring plots.

Table S1. Overview of the eight permanent plots studied. The typology of vegetation types follows Schmiedel (2002).

No.	Latitude	Longitude	Starting year	Vegetation type	Soil pH	Soil salinity [mS cm^{-2}]	Mean species richness on 25 m^2	Stone content in soil [weight %]
2837	31° 24’ 51.7’’	18° 19’ 01.1’’	1993	*Argyroderma fissum*-dominated community	7.4	9.32	6.9	16
2877	31° 24’ 45.2’’	18° 39’ 05.3’’	1993	*Drosanthemum diversifolium*-dominated community	6.4	3.02	11.0	17
2898	31° 24’ 53.6’’	18° 38’ 43.2’’	1993	*Oophytum nanum* community	4.7	1.74	8.6	62
3019	31° 24’ 52.0’’	18° 28’ 43.2’’	1993	*Oophytum nanum* community	6.3	2.92	13.6	58
3076	31° 24’ 57.0’’	18° 38’ 40.0’’	1993	*Oophytum nanum* community	6.8	7.81	8.4	37
3077	31° 24’ 57.0’’	18° 38’ 40.0’’	1993	*Argyroderma delaetii*-dominated community	7.5	9.74	14.8	31
3078	31° 24’ 57.0’’	18° 38’ 40.0’’	1993	*Aridaria serotina-Ruschia bolusiae* succulent shrub community	8.2	0.24	31.3	32
4677	31° 24’ 41.0	18° 39’ 04.7’’	1995	*Dactylopsis digitata* ssp. *digitata*-dominated community	7.4	7.73	6.1	10

Table S2. List of all vascular plant taxa found on the permanent plots, arranged by life form (LF; Ch = chamaephytes; G = geophytes; T = therophytes). Undetermined species are listed with their field name and the collection number of a specimen housed in the herbarium of the University of Hamburg (HBG). In the second column, information on the overall distribution of the taxa is given (Endemic = endemic to Knersvlakte; Endemic* = endemic to quartz fields; Endemic** = endemic to quartz fields of the Knersvlakte; Invasive = introduced from Australia). In the third column, families are given according to Germishuizen & Meyer (2003). The fifth column indicates the number of plots in which a taxon was found at least once. The following columns characterise the results of a linear regression of $\log_{10}$ (relative abundance) on year of record (n = data points used for the regression; R^2 = explained variance; p = probability; Sign. = significance level of the regression). The final column lists the long-term trend of annual rate of increase λ as estimated by the regression model. For each of the three life forms, summary statistics based on species are provided at the bottom.

LF	Distribution	Family	Species	Plots	n	Increment	R^2	p	Sign.	λ
Ch		Crassulaceae	*Adromischus marianae*	2	16	–0.0133	0.0138	0.665		0.9698
Ch		Portulacaceae	*Anacampseros filamentors* ssp. *namaquensis*	1	8	–0.0186	0.1017	0.599		0.9580
Ch		Portulacaceae	*Anacampseros lanceolata* ssp. *lanceolata*	2	16	0.0195	0.0407	0.454		1.0460
Ch	Endemic	Aizoaceae	*Antimima excedens*	1	8	–0.0358	0.4177	0.212		0.9208
Ch		Aizoaceae	*Antimima intervallaris*	1	8	0.0212	0.1384	0.533		1.0500
Ch		Aizoaceae	*Antimima watermeyeri*	2	16	0.0075	0.0213	0.589		1.0175
Ch	Endemic**	Aizoaceae	*Argyroderma delaetii*	6	48	0.0144	0.0102	0.496		1.0336
Ch	Endemic**	Aizoaceae	*Argyroderma fissum*	6	48	0.0123	0.0914	0.037	*	1.0288
Ch	Endemic**	Aizoaceae	*Argyroderma pearsonii*	4	32	0.0654	0.0959	0.085		1.1626
Ch		Aizoaceae	*Aridaria noctiflora*	1	8	0.0123	0.1865	0.460		1.0287
Ch		Asparagaceae	*Asparagus capensis*	1	8	–0.0177	0.1197	0.565		0.9601
Ch		Asparagaceae	*Asparagus suaveolens*	1	8	0.0405	0.2804	0.343		1.0978
Ch	Endemic	Aizoaceae	*Cephalophyllum framesii*	2	16	0.0431	0.2028	0.080		1.1044
Ch	Endemic**	Aizoaceae	*Cephalophyllum spissum*	7	56	0.0075	0.0176	0.330		1.0174
Ch	Endemic*	Aizoaceae	*Conophytum calculus* ssp. *calculus*	1	8	–0.0186	0.1017	0.599		0.9580
Ch	Endemic*	Aizoaceae	*Conophytum minutum* ssp. *minutum*	1	8	0.0239	0.2535	0.374		1.0567
Ch		Crassulaceae	*Crassula columnaris* ssp. *prolifera*	5	40	0.0533	0.1789	0.007	**	1.1307
Ch	Endemic*	Crassulaceae	*Crassula deceptor*	2	16	0.0264	0.0316	0.242		1.0627
Ch		Crassulaceae	*Crassula hirtipes*	1	8	0.1290	0.6247	0.077		1.3458
Ch		Crassulaceae	*Crassula muscosa* var. *muscosa*	2	16	–0.0154	0.0244	0.564		0.9651
Ch		Crassulaceae	*Crassula subaphylla* ssp. *virgata*	2	16	0.0273	0.0484	0.413		1.0650
Ch		Crassulaceae	*Crassula tomentosa* ssp. *tomentosa*	1	8	0.0097	0.0121	0.861		1.0226
Ch	Endemic**	Aizoaceae	*Dactylopsis digitata*	2	16	0.0146	0.4914	0.003	**	1.0342

LF	Distribution	Family	Species	Plots	*n*	Increment	R^2	*p*	Sign.	*λ*
Ch	Endemic	Aizoaceae	*Drosanthemum diversifolium*	6	48	0.0187	0.0942	0.034	*	1.0440
Ch		Aizoaceae	*Drosanthemum globosum*	2	16	–0.0185	0.0573	0.372		0.9583
Ch		Aizoaceae	*Drosanthemum pulverulentum*	1	8	0.1163	0.6638	0.060		1.3070
Ch		Aizoaceae	*Drosanthemum* spec. (Schmiedel 116576 HBG, ”glossy, lilac”)	3	24	0.0122	0.0185	0.526		1.0286
Ch		Aizoaceae	*Drosanthemum* spec. 5	1	8	0.0462	0.6247	0.077		1.1122
Ch	Endemic	Euphorbiaceae	*Euphorbia muricata*	1	8	0.0535	0.4886	0.158		1.1310
Ch		Aizoaceae	*Lampranthus watermeyeri*	1	8	0.1039	0.8479	0.008	**	1.2702
Ch	Endemic	Aizoaceae	*Malephora purpureo–crocea*	2	16	–0.0257	0.2485	0.049	*	0.9425
Ch	Endemic**	Aizoaceae	*Monilaria pisiformis*	1	8	–0.0920	0.6399	0.070		0.8091
Ch	Endemic**	Aizoaceae	*Oophytum nanum*	5	40	0.0163	0.0805	0.076		1.0383
Ch	Endemic**	Aizoaceae	*Oophytum oviforme*	2	16	0.0046	0.0021	0.865		1.0107
Ch		Asteraceae	*Othonna protecta*	2	16	–0.0290	0.0480	0.415		0.9354
Ch		Aizoaceae	*Phyllobolus nitidus*	1	8	–0.0239	0.0593	0.693		0.9464
Ch		Aizoaceae	*Psilocaulon dinteri*	1	8	0.0462	0.6247	0.077		1.1122
Ch		Aizoaceae	*Ruschia bolusiae*	1	8	–0.0119	0.4301	0.202		0.9729
Ch		Aizoaceae	*Ruschia subsphaerica*	2	16	–0.0109	0.0893	0.261		0.9751
Ch		Chenopodiaceae	*Salsola* spec. (Schmiedel 118975 HBG, “leafless, green”)	1	8	0.0693	0.6247	0.077		1.1730
Ch		Chenopodiaceae	*Salsola zeyheri*	6	48	0.0598	0.4155	<0.001	***	1.1476
Ch	Endemic**	Chenopodiaceae	*Salsola* spec. (Schmiedel 39488 HBG, “sericeous”)	6	48	0.0348	0.2414	<0.001	***	1.0834
Ch		Chenopodiaceae	*Salsola* spec. 1	1	8	0.0462	0.6247	0.077		1.1122
Ch	Endemic**	Chenopodiaceae	*Sarcocornia xerophila*	1	8	0.0366	0.6247	0.077		1.0879
Ch		Asteraceae	*Senecio aloides*	3	24	0.1081	0.3368	0.002	**	1.2825
Ch	Endemic**	Asteraceae	*Senecio sarcoides*	1	8	–0.0032	0.0007	0.967		0.9926
Ch		Aizoaceae	*Tetragonia fruticosa*	2	16	0.0081	0.0122	0.683		1.0188
Ch		Crassulaceae	*Tylecodon pearsonii*	2	16	0.0487	0.4024	0.008	**	1.1186
Ch	Endemic**	Crassulaceae	*Tylecodon pygmaeus*	8	64	0.0327	0.1501	0.002	**	1.0781
Ch		Crassulaceae	*Tylecodon reticulatus*	1	8	–0.0462	0.6247	0.077		0.8991
Ch		Zygophyllaceae	*Zygophyllum cordifolium*	2	16	–0.0148	0.0890	0.262		0.9665
Ch			**Mean (51 species)**			**0.0195**	**0.2484**			**1.0508**
Ch			**SD**			**0.0420**	**0.2431**			**0.1040**

LF	Distribution	Family	Species	Plots	*n*	Increment	R^2	*p*	Sign.	*λ*
Ch			**SE**			**0.0105**	**0.0608**			**0.0260**
Ch			**Min**			**–0.0920**	**0.0007**			**0.8091**
Ch			**Max**			**0.1290**	**0.8479**			**1.3458**
G		Iridaceae	*Gladiolus scullyi*	1	8	–0.0122	0.0433	0.738		0.9724
G		Hyacinthaceae	*Ornithogalum nanodes*	1	8	0.0128	0.0129	0.857		1.0299
G		Hyacinthaceae	*Ornithogalum* spec. 2	1	8	–0.0178	0.0543	0.706		0.9598
G	Endemic**	Asteraceae	*Othonna intermedia*	1	8	0.0733	0.6999	0.045	*	1.1839
G		Oxalidaceae	*Oxalis pes-caprae*	1	8	–0.0178	0.0543	0.706		0.9598
G	Endemic**	Aizoaceae	*Phyllobolus abbreviatus*	4	32	0.0468	0.1492	0.029	*	1.1138
G			**Mean (6 species)**			**0.0142**	**0.1690**			**1.0366**
G			**SD**			**0.0382**	**0.2641**			**0.0934**
G			**SE**			**0.0156**	**0.1078**			**0.0381**
G			**Min**			**–0.0178**	**0.0129**			**0.9598**
G			**Max**			**0.0733**	**0.6999**			**1.1839**
T		Asteraceae	*Amellus strigosus*	3	24	–0.0264	0.0352	0.380		0.9410
T	Invasive	Chenopodiaceae	*Atriplex lindleyi* ssp. *inflata*	5	40	–0.0233	0.0283	0.299		0.9478
T	Invasive	Chenopodiaceae	*Atriplex semibaccata*	1	8	–0.0057	0.0094	0.878		0.9870
T		Asteraceae	*Didelta carnosa*	5	40	–0.0418	0.0844	0.069		0.9082
T		Fabaceae	*Lotononis parviflora*	1	8	–0.0263	0.0433	0.738		0.9413
T		Aizoaceae	*Mesembryanthemum fastigiatum*	4	32	–0.1005	0.1232	0.049	*	0.7934
T		Aizoaceae	*Mesembryanthemum nodiflorum*	2	16	–0.0423	0.1235	0.182		0.9073
T		Asteraceae	*Foveolina dichotoma*	5	40	–0.0333	0.0254	0.326		0.9261
T		Asteraceae	*Rhynchopsidium pumilum*	4	32	–0.0120	0.0113	0.563		0.9728
T		Asteraceae	*Tripteris clandestina*	1	8	–0.0085	0.0094	0.878		0.9806
T			**Mean (10 species)**			**–0.0320**	**0.0493**			**0.9306**
T			**SD**			**0.0272**	**0.0448**			**0.0556**
T			**SE**			**0.0086**	**0.0142**			**0.0176**
T			**Min**			**–0.1005**	**0.0094**			**0.7934**

LF	Distribution	Family	Species	Plots	*n*	Increment	*R*²	*p*	Sign.	*λ*
T			**Max**			**–0.0057**	**0.1235**			**0.9870**