UNIVERSITY OF CAPE TOWN

Long-term vegetation change in the Succulent Karoo, South Africa following 67 years of rest from grazing.

by

Sebataolo John Rahlao

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Leslie Hill Institute for Plant Conservation
Department of Botany
University of Cape Town

Fitzpatrick Institute of African Ornithology
Department of Zoology
University of Cape Town

Supervisor: Prof. Timm Hoffman

ABSTRACT

Changes in species richness and vegetation composition in the diverse semi-arid Succulent Karoo vegetation of South Africa were investigated after 67 (1937-2004) years of rest from grazing at the Worcester Veld Reserve. Vegetation change in 70 plots at this 75 ha site was assessed using multi-variate ordination techniques. Changes in plant communities on termitaria sites were consistently greater than for adjacent off-termitaria sites and the north-facing slopes changed more than the south-facing slopes. There was a higher increase in diversity on off-termitaria than termitaria sites. On termitaria sites there was a general decrease in stem succulents, particularly *Euphorbia mauretanica* and an increase in long-lived evegreen shrubs such as *Pteronia incana* and *Asparagus suaveolens.* Most sites changed in a similar direction primarily determined by their association with termitaria and secondarily with aspect. These findings suggest a predictable and directional replacement sequence under changing disturbance (grazing) regimes in a semi-arid region.

KEY WORDS:
diversity; growth form; ordination; species richness; succession; termitaria.

INTRODUCTION

The dynamics of arid ecosystems have to be understood if they are to be managed for sustained species and rangeland conservation. This is particularly important given the limited resources for conservation. Most studies on vegetation dynamics are hindered by their short duration, which is usually not as long as the time scale of vegetation changes particularly in semi-arid regions where vegetation changes are notoriously slow (Noy-Meir 1973; Milton and Dean 1990; O'Connor and Roux 1995). Disturbance, particularly heavy grazing, has been found to have an ecological effect particularly in arid and semi-arid ecosystems (Dean and Milton 1999; Todd and Hoffman 1999; Valone *et al.* 2002). Grazing has been found to promote shifts in vegetation from grasslands to shrublands (O'Connor and Roux 1995) or leaf succulent shrublands to annuals and unpalatable or toxic perennial shrubs (Todd and Hoffman 1999).

In this study it was investigated whether resting a grazed rangeland at the Worcester Veld Reserve in the Succulent Karoo of South Africa, had led to the recovery of vegetation without any further management intervention. This is particularly important for species conservation as well as for rehabilitation because large parts of the semi-arid Karoo are already overgrazed (Wiegand and Milton 1996) and resources for rehabilitation and restoration are scarce or not available. Studies elsewhere have found that grazing significantly inhibited plant succession (Carmel and Kadmon 1999) and hence recovery. As a result rehabilitation of overgrazed shrublands has seldom been achieved by the withdrawal of livestock alone (Wiegand and Milton 1996). Cyclical replacement of species may, however, occur if historical conditions return (Yeaton 1978; Yeaton and Esler 1990).

The Succulent Karoo is a heterogeneous region with the presence of termitaria (known locally as heuweltjies), large circular earth mounds of up to 30 m in diameter and 1 m high (Armstrong and Siegfried 1990). These termitaria occur throughout the winter rainfall region of the western Cape (Lovegrove and Siegfried 1986) and particularly at the Worcester Veld Reserve (Midgley and Musil 1990). Several hypotheses exist about their origin with the popular hypotheses attributing their origin to the burrowing activities of termites, *Microhodotermes viator* (Lovegrove 1991) and enhancement through disturbance and fertilizing by other animals (Milton and Dean 1990). Termitaria sites have higher nutrient status, water holding capacity, organic matter and pH (Lovegrove 1991). This creates heterogeneighty in moisture and soil fertility (Milton and Dean 1990), particularly in the availability of nitrogen and phosphorus on the deeper and richer termitaria soils (Midgley and Musil 1990). As a result, termitaria support distinctive assemblages of plant and animal species (Knight *et al.* 1989; Milton and Dean 1990). In addition, large grazing mammals tend to concentrate and selectively graze these "nutrient islands" (Armstrong and Siegfried 1990) causing more disturbances on them than their neighbouring off-termitaria areas.

The time period (67 years) of this study is relatively long and has provided time for plant composition to change. The aim was to investigate how northern and southern termitaria and off-termitaria communities have changed in species composition and growth form between 1937 and 2004 following removal of all livestock from the Worcester Veld Reserve in 1937.

METHODS

Study site

This study was conducted at the Worcester Veld Reserve (WVR), which lies in the Worcester Robertson Valley, about 140 km east of Cape Town, South Africa (33°39'S and 19°27'E) at an altitude of 260-340 m above sea level (Figure 1). The area is 72 ha in extent and the landscape is comprised of Malmesbury shale-derived, shallow soils with exposed bedrock although soils are deeper on the termitaria and at the bottom of slopes (Smitherman and Perry 1990). The WVR lies within a Mediterranean climate region with a mean annual rainfall of 239 mm. Most of the rain falls between April and September with 15% of the rain falling in June. The northwestern part of the WVR is relatively drier and warmer while the southeastern side is relatively cooler and moister. The mean daily maximum temperature for the area is 24.8 °C.

The WVR was previously commonage and was declared a reserve in January 1935 (van Breda 1937) and has not been grazed by domestic livestock for at least 67 years although a few small antelope use the reserve from time to time.

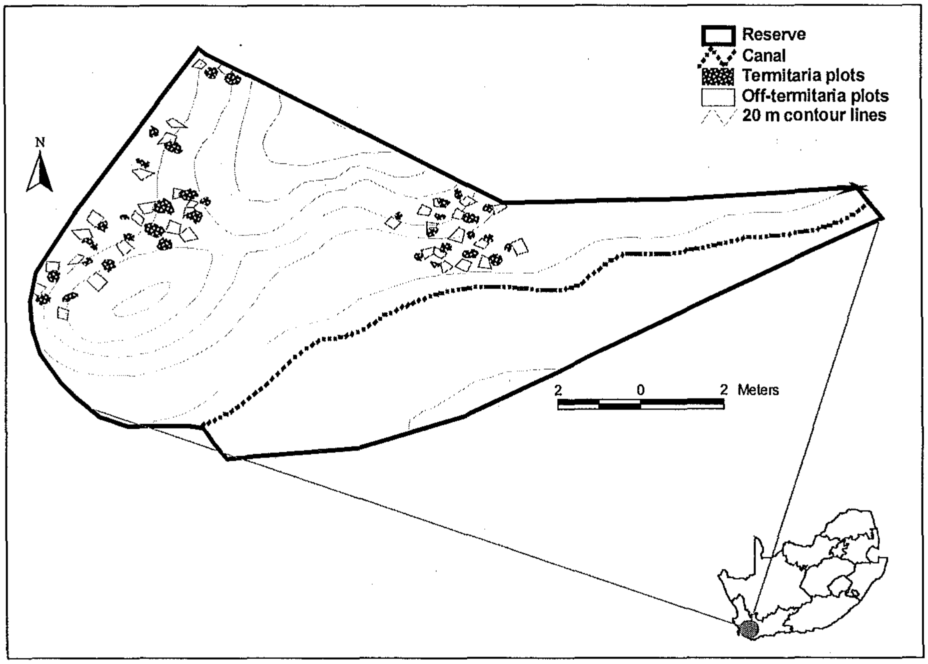

Figure 1 Map of The Worcester Veld Reserve showing the location of the 70 survey plots on the northern and southern slopes

Sampling design

After the WVR was declared a reserve in 1935, the reserve manager, Mr van Breda surveyed the vegetation. The methods he used in this initial survey are outlined in van Breda (1937). His herbarium samples are still present at the reserve. The same methodology used by van Breda (1937) was adopted and his plots were re-established (some of which still retained his markings) by superimposing his survey map onto aerial photographs of the area. This was done by aligning the position of termitaria drawn on his survey map with those in the aerial photograph.

van Breda divided the reserve into 78 one morgen plots (van Breda, 1937) with each morgen plot divided into nine squares, each approximately 34 x 34 yards (= 31.1 x 31.1 m). A total of 70 plots on termitaria and their adjacent off-termitaria communities were re-sampled in 2004 (Figure 1). Off-termitaria plots were each 900 m^2 (30 x 30 m) and termitaria plots differed depending on the size and shape of the termitaria studied. Plot coordinates were determined using a hand held Garmin 70 GPS. A study undertaken at the adjacent Worcester Botanical Gardens (Smitherman and Perry 1990) found that there was a marked difference between the northern and southern aspects. The vegetation was taller with more plant cover and mosses as well as annuals on the southern aspect and lower species richness with sparser and shorter vegetation on the northern aspect. To address these differences both northern aspect (40 plots) and southern aspect (30 plots) sites were sampled.

Species richness and percent cover were measured by counting the number of different species and estimating their total cover in each plot. The following physical variables were also recorded for each plot; aspect (^{0}), slope (^{0}), soil depth (cm), rock cover (%), stone cover (%), lichens (%), mosses (%), annuals (%), geophytes (%) and litter (%). Aspect and slope were measured using a compass and Abney level respectively. Soil depth was measured by hammering a 1 m metal rod at five points within each plot until it hit bedrock or could not penetrate any further. An average of the five points was used.

Data Analysis

All the species recorded were assigned to the following functional types based on their growth form: grass, deciduous shrub, evergreen shrub, leaf succulent small (<25 cm), leaf succulent large (>25 cm), stem succulent and tree. This assisted in the comparison of growth forms between different landscape units and the growth form changes over time. Nonmetric Multidimensional Scaling (NMS) ordination technique was used to examine plant community patterns and their relationships with the environmental variables. The data was transformed by excluding rare (that occurred less than three times) species in the area using PC-ORD program (McCune and Mefford 1999). The data was then relativized to put species and environmental variables (measured at different units) on an equal footing (McCune and Grace 2002).

A Wilcoxon Signed Rank Test was used to determine the differences in species richness in all the plots between 1937 and 2004. A Kruskal-Wallis one-way ANOVA and Dunn's multiple comparisons test were used to test for differences in the abiotic variables as well as percent cover and species richness between plots and over time. Student's t-test was used to investigate the differences in plant growth form across the landscape and over time. All statistical tests were performed using Statistica (StatSoft Inc. 2003).

RESULTS

Patterns of termitaria and off-termitaria vegetation in 2004

The Nonmetric Multidimensional Scaling (NMS) ordination of 2004 data showed the survey plots to be different depending on aspect and whether they were located on termitaria or not (Figure 2a). *Euphorbia mauretanica, Euphorbia burmannii* and *Lycium cinereum* were dominant on termitaria plots but did not show preference for either aspect. *Aloe microstigma*, *Psilocaulon sp.*, *Crassula subaphylla, Pentzia incana*, *Tripteris sinuatum* and *Galenia africana* dominated termitaria plots on the northern aspect. *Tylecodon paniculatus, Asparagus suaveolens* and *Pteronia incana* were consistently dominant on termitaria plots on the southern aspect. *Senecio corymbiferus* and *Ruschia caroli* were common on both termitaria and off-termitaria plots in 2004 irrespective of aspect. Off-termitaria plots on both aspects were dominated by *Pteronia paniculata* and *Felicia filifolia*. *Adromischus mammalaris* and *Elytropappus rhinocerotis* were also common on all off-termitaria plots in 2004. *Crassula rupestris*, *Hirpicium integrifolium* and *Senecio radicans,* however, were more common on off-termitaria plots on the northern aspect while *Thesium edule*, *Tetragonia hirsuta*, and *Aridaria sp.* were more common on the southern aspect.

The sample plots appeared strongly differentiated along key environmental axes (Figure 2b and Table 1). Termitaria plots had significantly deeper soils particularly on the northern aspect. They were also associated with higher annual plant cover, particularly on the southern aspect. There were more dead plants on termitaria plots, particularly on the southern aspect. Termitaria plots on both aspects had high vegetation cover but this did not differ significantly from off-termitaria plots on the southern aspect.

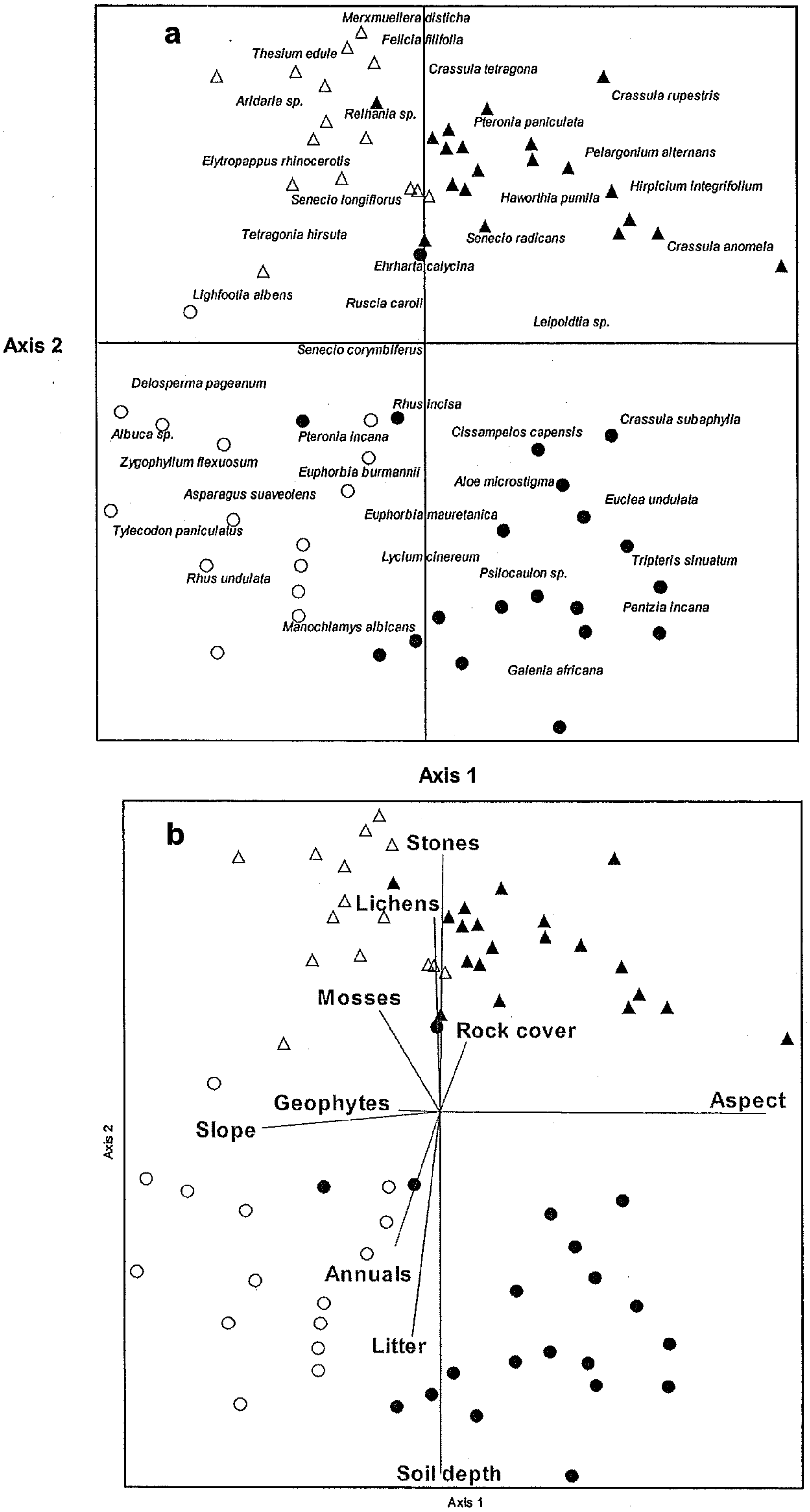

Figure 2: Nonmetric Multidimensional Scaling (NMS) ordination diagram of plots sampled in 2004 with **a)** Important species influencing the ordination **b)** A biplot of the data collected in 2004 and the vectors illustrating the measured abiotic variables. Circles represent termitaria plots on the southern aspect; dots represent termitaria plots on the northern aspect. Open triangles represent off-termitaria plots on the southern aspect while filled triangles represent off-termitaria plots on the northern aspect.

Off-termitaria plots were associated with high rock and stone cover and there was no significant difference in these variables between the northern and southern aspect. Lichens were common on off-termitaria plots and significantly higher on the southern aspect. Mosses were persistent on off-termitaria plots on the southern aspect. Off-termitaria plots had a significantly higher number of species particularly on the southern aspect.

Table 1: Mean (± stdev) values for biotic and abiotic descriptors of 70 termitaria and off-termitaria plots located on southern and northern aspect at the Worcester Veld Reserve in 2004. Significant differences between values in a row are denoted by dissimilar superscripts using Kruskal Wallis one-way ANOVA and Dunn's multiple comparisons test at the $p<0.05$ level.

	Termitaria		**Off-termitaria**	
Variable	**South (N=15)**	**North (N=20)**	**South (N=15)**	**North (N=20)**
Slope (^{0})	16.2 ± 3.5^{c}	9.7 ± 5.9^{b}	15.6 ± 3.7^{c}	5.5 ± 4.0^{a}
Soil depth (cm)	26.3 ± 6.9^{b}	34.5 ± 11^{c}	8.1 ± 3.0^{a}	9.3 ± 5.5^{a}
Rock cover (%)	0.5 ± 0.5^{a}	0.5 ± 0.9^{a}	5.3 ± 2.7^{b}	6.1 ± 9.2^{b}
Stone cover (%)	1.5 ± 1.1^{a}	1.9 ± 1.3^{a}	17.4 ± 9.7^{b}	15.1 ± 8.3^{b}
Lichens (%)	0.0 ± 0.0^{a}	0.01 ± 0.03^{a}	6.5 ± 4.1^{c}	2.1 ± 2.5^{b}
Mosses (%)	0.7 ± 0.5^{c}	0.01 ± 0.02^{a}	5.5 ± 4.2^{d}	0.14 ± 0.3^{b}
Annuals (%)	3.5 ± 4.0^{c}	1.3 ± 1.8^{b}	0.01 ± 0.03^{a}	0.00 ± 0.0^{a}
Geophytes (%)	0.3 ± 0.4^{c}	0.01 ± 0.0^{a}	0.3 ± 0.4^{c}	0.06 ± 0.1^{b}
Litter (%)	9.7 ± 5.8^{c}	6.3 ± 4.9^{b}	2.6 ± 1.5^{a}	2.3 ± 1.0^{a}
Vegetation cover (%)	76.9 ± 10.2^{b}	76.9 ± 20.2^{b}	71.3 ± 9.5^{b}	57.4 ± 9.0^{a}
Number of species (n)	21 ± 4.2^{a}	23 ± 4.6^{a}	33 ± 6.9^{b}	29 ± 5.8^{b}

Differences in vegetation between 1937 and 2004

The ordination of termitaria plots showed a diversification in species composition in 2004 relative to 1937 (Figure 3a). Termitaria plots were clustered together and there were few differences in species composition between southern and northern aspects in 1937. *Pteronia paniculata* and *Ruschia caroli* were dominant on the edges of termitaria plots irrespective of whether they occurred on the southern or northern aspects in both 1937 and 2004 (Table 2). *Crassula rupestris*, *Galenia africana* and *Euphorbia mauretanica* were more common on termitaria plots in 1937 particularly on the northern aspect. *Aridaria sp.* and *Delosperma pageanum* were more common species on termitaria plots on the southern aspect in 1937.

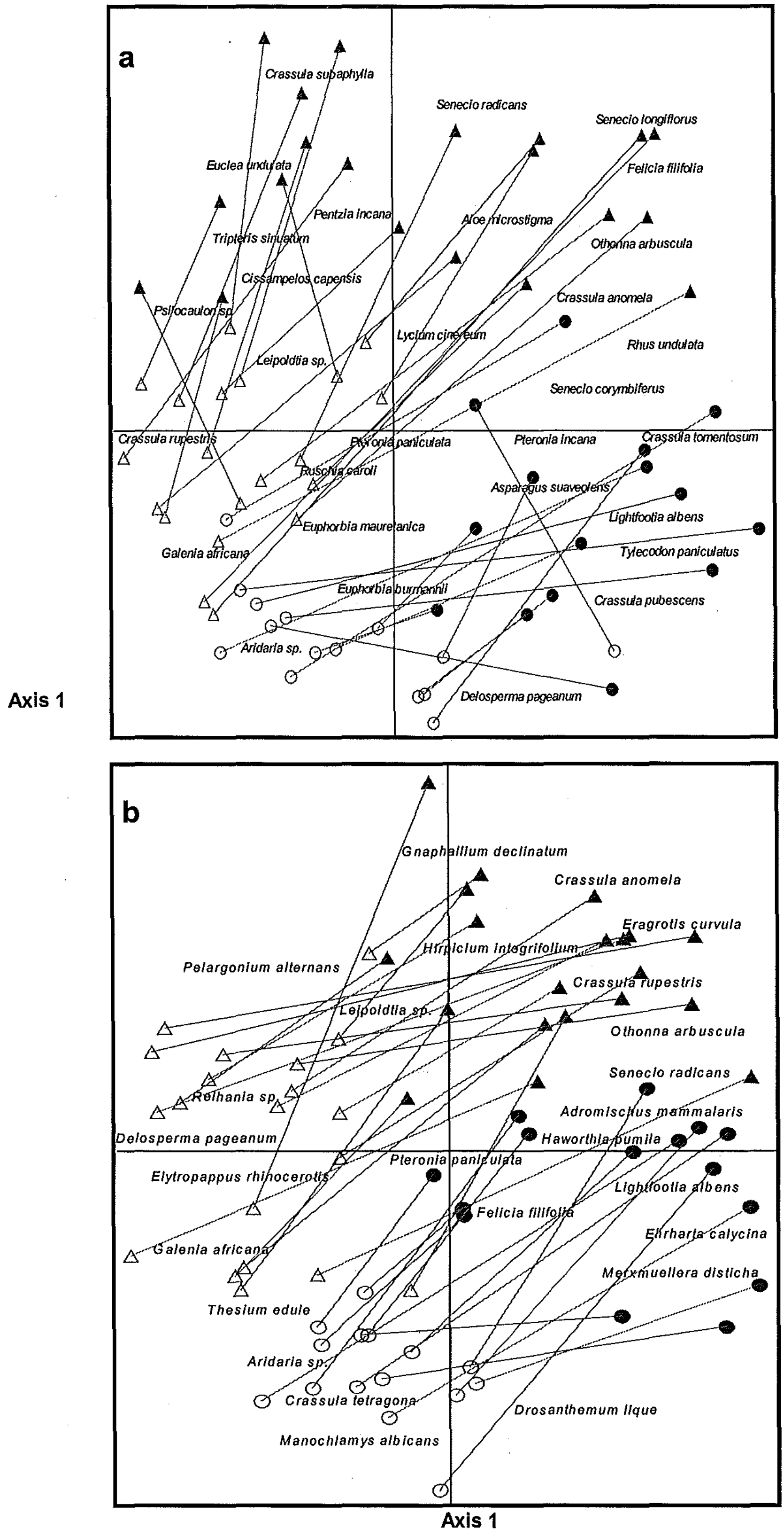

Figure 3: Nonmetric Multidimensional Scaling (NMS) ordination diagram showing how the plots have changed over 67 years relative to each other and the species that have influenced the change the most **a)** termitaria plots sampled in 1937 and 2004 and **b)** off-termitaria plots sampled in 1937 and 2004. The most influential species have been labelled. Open triangles and circles represent plots in 1937 on the northern and southern aspects respectively. Filled triangles and dots represent northern and southern aspect plots sampled in 2004. The length of the line represents the amount of change between 1937 and 2004.

Table 2: The mean percent cover of species occurring more than five times in the 70 plots and with a cover value higher than 0.01%. A Wilcoxon Matched Paired Test was used to determine the change in species composition for termitaria and off-termitaria sites between 1937 and 2004. * = $p < 0.05$

Species	**Growth form**	**Termitaria (n=35)**			**Off-termitaria (n=35)**		
		1937	**2004**		**1937**	**2004**	
Chrysocoma ciliata	deciduous shrub	0.2	0.0		0.7	0.0	*
Chrysocoma coma-aurea	deciduous shrub	1.0	0.2	*	0.1	0.0	*
Cissampelos capensis	deciduous shrub	0.2	0.3	*	0.0	0.0	
Eriocephalus ericoides	deciduous shrub	0.1	0.1		0.0	0.0	
Felicia cf fruticosa	deciduous shrub	0.0	0.0		0.0	0.1	*
Felicia filifolia	deciduous shrub	0.0	0.0		0.6	1.0	*
Galenia africana	deciduous shrub	18.8	2.7	*	2.2	0.0	
Lebeckia cytisoides	deciduous shrub	0.0	0.0		0.1	0.1	
Lightfootia albens	deciduous shrub	0.2	0.4		0.4	1.0	
Lycium cinereum	deciduous shrub	1.2	1.9	*	0.0	0.0	
Manochlamys albicans	deciduous shrub	0.1	0.2		0.1	0.0	
Pentzia incana	deciduous shrub	0.7	1.0		0.1	0.0	
Selago ramosissima	deciduous shrub	0.2	0.0	*	0.3	0.0	*
Thesium edule	deciduous shrub	0.0	0.0		0.5	0.1	*
Tripteris sinuatum	deciduous shrub	0.4	0.4		0.0	0.1	*
Zygophyllum flexuosum	deciduous shrub	0.1	0.2		0.2	0.1	
Total cover		**23.1**	**7.6**	*	**5.2**	**2.7**	
Aspalathus acuminata	evergreen shrub	0.0	0.0		0.2	0.0	*
Asparagus fasciculatus	evergreen shrub	0.0	0.1		0.0	0.0	
Asparagus suaveolens	evergreen shrub	2.2	3.4		0.1	0.1	
Atriplex nummularia	evergreen shrub	0.0	0.1	*	0.0	0.0	
Elytropappus rhinocerotis	evergreen shrub	0.4	0.1		2.7	1.1	*
Gnaphilium declinatum	evergreen shrub	0.0	0.1	*	0.0	0.0	
Helichrysum rosum	evergreen shrub	0.0	0.2	*	0.0	0.0	*
Hermannia cuneifolia	evergreen shrub	0.2	0.3		0.0	0.0	
Hirpicium integrifolium	evergreen shrub	0.0	0.1		0.9	1.9	*
Indigofera sessifolia	evergreen shrub	1.1	0.0	*	0.2	0.0	
Microloma sagittatum	evergreen shrub	0.0	0.0		0.1	0.0	

Passerina sp.	evergreen shrub	0.0	0.0		0.2	0.7	*
Pelargonium alternans	evergreen shrub	0.3	0.1		2.0	1.7	
Pteronia incana	evergreen shrub	6.2	18.4	*	0.1	0.2	
Pteronia paniculata	evergreen shrub	2.2	1.4		32.7	26.9	*
Relhania sp.	evergreen shrub	0.0	0.0		2.3	0.8	*
Sutera glabrata	evergreen shrub	0.0	0.0		0.2	0.0	
Sutherlandia frutescens	evergreen shrub	0.1	0.0		0.0	0.0	
Total cover		**12.8**	**24.3**	*	**41.8**	**33.5**	*
Ehrharta calycina	grass	0.1	0.2		0.5	0.8	*
Eragrostis curvula	grass	0.0	0.0		0.0	0.1	
Merxmuellera disticha	grass	0.0	0.0		0.0	0.1	*
Ischyrolepis gaudichaudianus	grass (restio)	0.0	0.0		0.2	0.2	
Total cover		**0.1**	**0.2**		**0.7**	**1.1**	
Aloe microstigma	leaf succulent large	0.4	5.9	*	0.2	0.7	*
Aridaria sp. (grey)	leaf succulent large	3.5	0.0	*	0.0	0.0	
Aridaria sp.(red)	leaf succulent large	0.1	0.0		3.5	0.1	*
Cotyledon orbiculata	leaf succulent large	0.2	0.1		0.1	0.0	
Crassula cotyledonis	leaf succulent large	0.0	0.0		0.0	0.1	*
Crassula rupestris	leaf succulent large	0.1	0.0		0.5	0.4	
Crassula tomentosum	leaf succulent large	0.0	0.0		0.1	0.0	
Delosperma pageanum	leaf succulent large	1.0	0.2	*	0.1	0.0	
Drosanthemum lique	leaf succulent large	1.7	0.2	*	1.1	0.0	
Drosanthemum speciosum	leaf succulent large	0.0	0.0		0.0	0.4	*
Lampranthus haworthii	leaf succulent large	0.1	0.2		1.4	0.8	
Leipoldtia sp	leaf succulent large	5.4	2.9	*	7.0	4.0	
Ruschia caroli	leaf succulent large	10.6	5.3	*	29.0	11.8	*
Senecio corymbiferus	leaf succulent large	0.2	0.8	*	0.5	0.9	*
Tetragonia fruticosa	leaf succulent large	0.1	0.1		0.6	0.2	*
Tetragonia hirsuta	leaf succulent large	0.0	0.1	*	2.8	0.5	*
Total cover		**23.3**	**15.9**	*	**46.9**	**19.8**	*
Adromischus mammalaris	leaf succulent small	0.0	0.0		0.0	0.2	*
Crassula anomela	leaf succulent small	0.0	0.0		0.0	0.3	*
Crassula muscosa	leaf succulent small	0.1	0.1		0.0	0.1	
Crassula pubescens	leaf succulent small	0.0	0.0		0.0	0.1	*

Crassula sp.	leaf succulent small	0.4	0.0	*	0.4	0.0	
Crassula subaphylla	leaf succulent small	0.0	0.2	*	0.0	0.1	
Crassula tetragona	leaf succulent small	0.1	0.0		0.4	0.1	
Haworthia herbacea	leaf succulent small	0.0	0.0		0.0	0.2	*
Haworthia pumila	leaf succulent small	0.0	0.0		0.0	0.1	*
Mesembryanthemum haworthia	leaf succulent small	0.0	0.0		2.0	0.1	*
Prenia pallens	leaf succulent small	0.3	0.0		0.0	0.0	
Senecio aizoides	leaf succulent small	0.0	0.0		0.0	0.1	*
Senecio radicans	leaf succulent small	0.0	0.1	*	0.1	0.2	*
Total cover		**0.9**	**0.6**		**2.9**	**1.6**	
Euphorbia burmanni	stem succulent	20.2	4.4	*	1.0	0.6	
Euphorbia mauritanica	stem succulent	20.0	2.6	*	0.8	0.2	
Euphorbia nesemanni	stem succulent	0.0	0.0		0.3	0.1	
Othonna arbuscular	stem succulent	0.0	0.0		0.1	1.5	*
Othonna carnosa var. carnosa	stem succulent	0.0	0.0		0.1	0.0	
Psilocaulon sp.	stem succulent	1.8	1.2	*	0.2	0.0	
Quaqua mammilaris	stem succulent	0.0	0.0		0.0	0.0	
Sarcostemma viminale	stem succulent	0.0	4.2	*	0.0	0.1	*
Senecio longiflorus	stem succulent	0.0	0.1		0.0	0.2	*
Senecio succulentus	stem succulent	0.0	0.0		0.0	0.1	*
Tylecodon paniculatus	stem succulent	3.8	6.3	*	0.4	0.1	
Total cover		**45.8**	**18.9**	*	**2.9**	**3.0**	
Dodonaea angustifolia	tree	0.0	0.0		0.3	0.5	
Euclea undulata	tree	3.6	3.2	*	0.4	0.2	
Rhus incisa	tree	0.7	2.4	*	0.6	0.7	
Rhus undulata	tree	0.0	2.4	*	0.1	0.1	
Total cover		**4.4**	**8.0**	*	**1.3**	**1.5**	

Aloe microstigma, Euclea undulata and *Pentzia incana*, were more common on termitaria plots in 2004, particularly on the northern aspect. *Asparagus suaveolens*, *Lightfootia albens* and *Tylecodon paniculata* were more common species on termitaria plots on the southern aspect in 2004. Termitaria plots on the northern aspect were more scattered in ordination space in 2004 than on the southern aspect.

Off-termitaria plots differed significantly in composition between southern and northern aspects in 1937 and the pattern was similar in 2004 (Figure 3b; Table 2). *Manochlamys albicans, Aridaria sp.* and *Crassula tetragona* were common on southern aspect, off-termitaria plots in 1937 while *Relhania sp., Galenia africana* and *Elytropappus rhinocerotis* were common on the northern aspect. More species were found on both aspects on off-termitaria plots in 2004. *Crassula anomela, Othonna arbuscula, Hirpicium integrifolium* and *Eragrostis curvula* were common on the northern aspect while *Felicia filifolia, Adromischus mammalaris, Merxmuellera disticha* and *Ehrharta calycina* were common on off-termitaria plots on the southern aspect in 2004.

Table 3: The mean (± stdev) percent cover of all species and mean species richness (± stdev) in 1937 and 2004 for termitaria and off-termitaria plots on southern and northern aspects of the Worcester Veld Reserve. A Wilcoxon Signed Rank Test was used to determine differences between sampling dates; * = p<0.01, ** = p<0.001

Landscape unit		Mean total % cover		Mean species richness	
	N	1937	2004	1937	2004
Termitaria, southern aspect	15	102 ± 12.0	77 ± 10.2*	16 ± 3.5	21 ± 4.3*
Termitaria, northern aspect	20	120 ± 24.4	77 ± 20.2*	17 ± 3.5	23 ± 4.5**
Off-termitaria, southern aspect	15	107 ± 15.6	71 ± 9.5*	21 ± 3.8	33 ± 7.2*
Off-termitaria, northern aspect	20	97 ± 19.1	57 ± 9.0*	14 ± 4.4	29 ± 5.9**

All plots had changed significantly in species richness and percent vegetation cover between 1937 and 2004 (Table 3). More change occurred on the northern aspect on both termitaria and off-termitaria sites. The change was due to the increase in number of species in 2004 relative to 1937. The percent vegetation cover decreased on termitaria and off-termitaria plots between 1937 and 2004 on both the southern and northern aspects.

Growth forms

The percent cover of three growth forms changed significantly on northern aspect termitaria between 1937 and 2004 (Figure 4a). There was a significant decrease in stem succulents over this period, particularly in the cover of *Euphorbia mauritanica, Euphorbia burmannii* and *Psilocaulon sp*. Deciduous shrubs such as *Galenia africana* and *Pentzia incana* declined on northern aspect termitaria plots between 1937 and 2004 although not significantly. The percent cover of large leaf succulents (e.g. *Aloe microstigma* and *Leipoldtia sp*) increased significantly on the northern aspect termitaria plots between 1937 and 2004. Similarly the cover of evergreen shrubs (e.g. *Pteronia incana* and *Asparagus suaveolens*) increased significantly between 1937 and 2004. Tree cover (e.g. *Rhus spp.*) also increased but not significantly on termitaria plots on the northern aspect.

There was more change in growth forms on the southern aspect termitaria plots between 1937 and 2004 (Figure 4b). There was a significant decrease in the cover of stem succulents (e.g. *E. mauretanica* and *E. burmannii*), and deciduous shrubs (e.g. *Galenia africana and Pentzia incana*) in 2004. Trees (e.g. *Rhus incisa* and *Rhus undulata*) and evergreen shrubs (*Pteronia incana* and *Asparagus suaveolens*) increased significantly in cover on the southern aspect termitaria in 2004. Grasses were never in abundance on the southern aspect termitaria. Large leaf succulents (e.g. *Aridaria spp., Ruschia caroli* and *Dronsanthemum lique*) decreased in cover although not significantly.

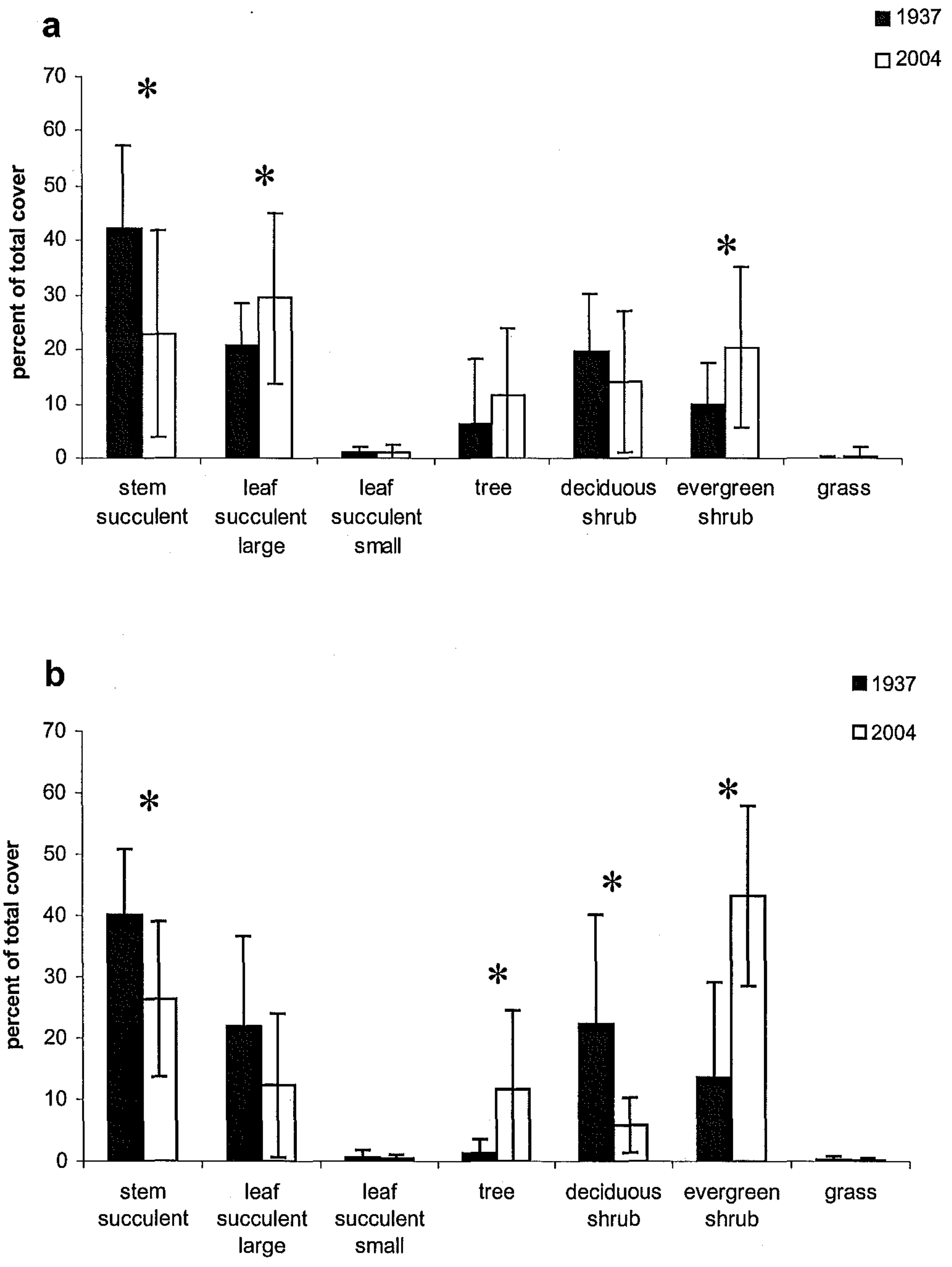

Figure 4: Mean percent cover for each growth form on termitaria plots in 1937 and 2004 on **a)** northern aspect and **b)** southern aspect. Student's t-test was used to determine differences in the percent cover within a growth form between the two sampling sites. ∗ = $p<0.05$.

Two growth forms on off-termitaria plots changed significantly in cover between 1937 and 2004 on the northern aspect (Figure 5a). There was a significant decrease in cover of large leaf succulents (e.g. *Ruschia caroli, Aridaria sp.* and *Leipoldtia sp.*). Stem succulents (e.g. *Othonna arbuscula*) were never common on northern off-termitaria plots in 1937 but increased significantly in 2004. Evergreen shrubs (e.g. *Pteronia paniculata*, *Relhania sp.*, and *Elytropappus rhinocerotis*) increased although not significantly in cover between 1937 and 2004. Other growth forms (small leaf succulents, trees, deciduous shrubs and grasses) were not dominant on off-termitaria plots either in 1937 and 2004.

Large leaf succulents (e.g. *Ruschia caroli*, *Aridaria spp.*, *Tetragonia hirsuta* and *Senecio corymbiferus)* decreased significantly in cover between 1937 and 2004 for off-termitaria plots on southern aspects (Figure 5b). Evergreen shrubs (e.g. *Relhania sp.* and *Pteronia paniculata*) increased significantly. None of the other growth forms changed significantly between 1937 and 2004 on off-termitaria plots on the southern aspect.

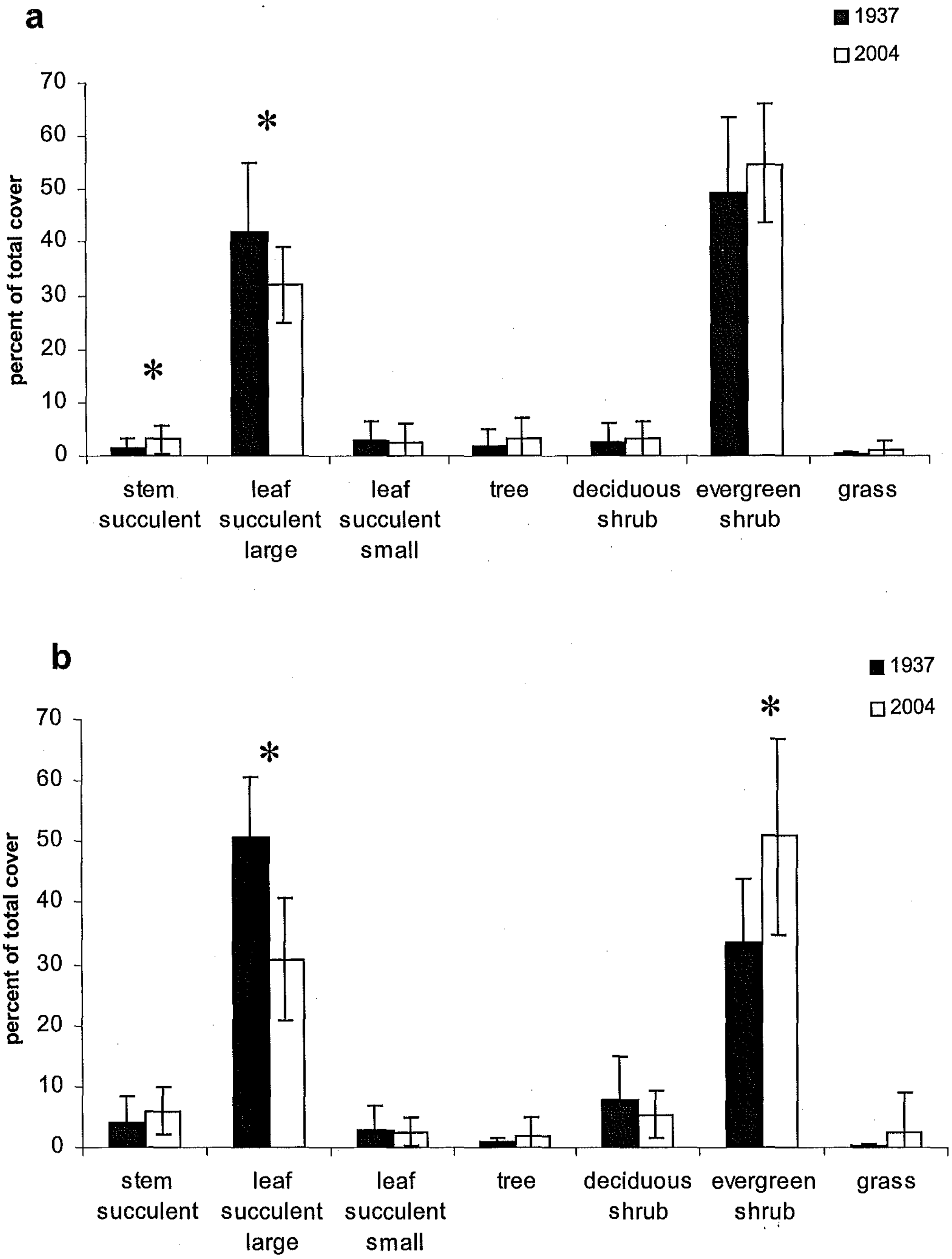

Figure 5: Mean percent cover for each growth form on off-termitaria plots in 1937 and 2004 on **a)** northern aspect and **b)** southern aspect. Student's t-test was used to determine differences in the percent cover within a growth form between the two sampling dates. * = $p<0.05$.

DISCUSSION

The influence of termites and aspect on arid ecosystems

Several studies have documented the role of termites (*Microhodotermes viator*) in influencing soil properties and vegetation composition (Lovegrove and Siegfried 1986; Cox *et al.* 1987; Milton and Dean 1990; Lovegrove 1991; Moore and Picker 1991) in the Succulent Karoo. The results of this study at the Worcester Veld Reserve confirm the differences in abiotic and biotic variables between termitaria and off-termitaria reported elsewhere (Knight *et al.* 1989; Milton and Dean 1990; Midgley 2002). Termitaria sites have deeper and more nutrient-rich soils and a higher proportion of trees, stem succulents and deciduous shrubs than adjacent off-termitaria sites (Midgley and Musil 1986). Slow growing and stress tolerant evergreen shrubs such as *Pteronia paniculata* and *Hirpicium integrifolium* and large leaf succulent shrubs such as *Ruschia caroli*, however, dominate the nutrient-deficient soils of off-termitaria sites.

This work highlights the role that aspect plays in influencing vegetation composition and cover. Smitherman and Perry (1990) have described distinct plant assemblages associated with aspect at the Karoo National Botanic Garden Reserve in Worcester a few kilometres from the Worcester Veld Reserve. This study confirms their results and shows that the hotter north-facing slopes have fewer species and a lower cover of vegetation with fewer annuals. There is, however, a higher cover of stem and leaf succulents (e.g. *Euphorbia spp*. and *Aloe microstigma*), particularly on the deeper termitaria soils. Taller and high vegetation cover and a greater incidence of annuals, however, are characteristic of the cooler south-facing slopes. There is also a higher cover of evergreen shrubs (e.g. *Pteronia spp*. and *Asparagus suaveolens*).

Long-term change in desert ecosystems

While long-term studies on vegetation change do exist for some areas (Turner 1990; Valone *et al.* 2002; Goldberg and Turner 1986; Carmel and Kadmon

1999), there are few studies for semi-arid South Africa (O'Connor and Roux 1995). Those that do exist (Wiegand and Milton 1996; Yeaton and Esler 1995) have relied largely on models to explain the long-term dynamics of vegetation composition and change in the Succulent Karoo. Earlier ideas of vegetation change in the Karoo adopted the Clementsian succession paradigm developed for more mesic areas in North America (Acocks 1953). This view proposes that the vegetation of the Succulent Karoo is climatically determined and reaches a climax condition under low grazing pressure (Roux and Vorster 1983). As grazing pressure increases, the vegetation changes and retreats along a predictable successional replacement sequence until it is dominated by short-lived weedy and unpalatable species. A release from grazing would propel the vegetation back to its climax state (Roux and Vorster 1983).

Another view proposed by Yeaton and Esler (1990) is that there is a cyclical replacement of plant guilds under changing disturbance regimes. This model suggests that further plant turnover on termitaria will continue to enrich the concentration of nutrients there. Once grazing ceases, the surficial organic materials would be eroded off the mounds thereby changing the pH and chemical (e.g. calcium) composition downslope resulting in a change in vegetation composition. This interchange of conditions eventually leads to a cyclical replacement of species depending on grazing regimes and chemical concentrations on termitaria sites.

A third model of vegetation change in the Karoo suggests that vegetation changes are unpredictable on short time scales (years) and episodic on long time scales in response to a combination of factors such as climate, grazing pressure, rare events and changed disturbance regimes (Wiegand and Milton 1996). This model argues that even the availability of long-term records of the dynamics of a semi-arid plant community would have limited predictive value mainly due to the high stochasticity of this system. The model predicts that a dynamic inertia exists in overgrazed rangeland. Once a long-lived species has established an abundant population, it will persist for a long-time and occupy sites that otherwise could serve as establishment sites for competing species. The model suggests that without some form of intervention, a low probability exists that Succulent Karoo vegetation would rehabilitate itself in 60 years by simply removing grazing animals. This view rejects the Clementsian succession paradigms, which suggests resting restores what grazing has removed (Roux and Vorster 1983).

Contrary to the views of Wiegand and Milton (1996) the results from this study show that vegetation at the Worcester Veld Reserve has changed significantly between 1937 and 2004 as a direct result of the removal of domestic livestock from the area. No attempt to rehabilitate the vegetation of the WVR was undertaken over this time period and there is little indication that rainfall patterns have changed since 1937 (Agricultural Research Council, unpublished data). The best explanation is that the absence of grazing animals from the area has promoted the increase in some growth forms and the decline in others. There is also no evidence of a cyclical succession process (Yeaton and Esler 1990). Instead, most plots have changed in a similar direction in ordination space, determined primarily by its association with a termite mound and secondarily by its aspect. Northern aspect termitaria plots have changed the most while off-termitaria plots on the southern aspect have changed the least. There has been a general increase in trees and evergreen shrubs and a decrease in deciduous shrubs and stem succulents particularly of *Euphorbia mauretanica* – a species which usually increases under heavy disturbance (Knight *et al.* 1989).

There has also been an increase in diversity at all sites but this increase has been highest for off-termitaria sites. The increase in small, wind-dispersed leaf succulents within the Crassulaceae, Asphodelaceae and Asteraceae is particularly noticeable. These species (*Crassula spp., Adromischus mammalaris, Haworthia spp., Senecio radicans*) are particularly susceptible to grazing impact and would have been significantly impacted under the high grazing pressure prior to 1937.

Limitations of the study

There are a number of limitations associated with this study. The absence of sites which have not been grazed at all make it difficult to compare the changes at the Worcester Veld Reserve with a putative pristine landscape. Similarly, the influence of climatic factors over the last 67 years would have been better assessed if an adjacent site was found which had been grazed continuously since 1937. While the lack of controls is regrettable this study has still provided important insights into the nature and extent of vegetation change in the Succulent Karoo when rested from grazing over long time periods. It is essential to encourage long-term studies as they provide valuable insights for the management of rangelands, particularly in arid and semi-arid ecosystems for sustained species conservation and rangeland management.

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