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How does grazing intensity affect different vegetation types in arid Succulent Karoo, South Africa? Implications for conservation management

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ABSTRACT

The Knersvlakte in the Succulent Karoo Biome (South Africa) is known for its high plant diversity and endemism. In the course of establishing a conservation area there, we assessed baseline data for future management. We investigated the effects of grazing on the vegetation in terms of species diversity and composition as well as reproduction of selected species. Data were sampled on four adjacent farms, which were ungrazed, moderately or intensively grazed by sheep and goats. The data were collected in 27 quartz and 24 non-quartz plots, representing two major habitat types of the region. Within each of the 1000-m^2 plots, 100 subplots of 400 cm^2 size were sampled. ANOVAs revealed that species richness and abundance of endemic species on quartz fields decreased with grazing. Abundance of annuals did not increase significantly due to grazing. Fidelity analyses indicated that species composition differed between grazing intensities and that the ungrazed and moderately grazed plots both contained unique locally endemic habitat specialists. Reproduction of two endemic dwarf shrubs *Drosanthemum schoenlandianum* and *Argyroderma fissum* (both Aizoaceae) increased under moderate grazing, which in the case of *D. schoenlandianum* was interpreted as an effect of grazing. We attribute the low number of seedlings and annuals on the moderately grazed farm to lower seasonal rainfall on these plots. From a conservation perspective, no or moderate grazing appear to be necessary to preserve plant diversity and vegetation patterns, and their underlying processes.

1. Introduction

Growing awareness in recent decades of the irreplaceable loss of biodiversity as well as of the ecological and economic value of ecosystem functions and services has modified the goals of conservation planning. The recently developed concept of systematic conservation planning aims to sustainably conserve current biodiversity. This it does by taking into account patterns and processes that allow the maintenance of biological assemblages, species and populations, and ecosystem dynamics and adaptation (Margules and Pressey, 2000).

Recent conservation planning for the biodiversity hotspots of South Africa (Myers et al., 2000), such as the Cape Floristic Region and Succulent Karoo, follow the concept of systematic conservation planning (Cowling and Pressey, 2003; Desmet, 2004; Desmet et al., 1999; Pressey et al., 2003). Within the Succulent Karoo, the Knersvlakte has been recognized as one of the highest conservation priority areas in South Africa due to its unique flora and its high diversity and endemism (Desmet et al., 1999; Hilton-Taylor and Le Roux, 1989). Currently, the prospective Knersvlakte Conservation Area has a size of 62,000 ha managed by the provincial nature conservation authority, CapeNature. By incorporating more farms, CapeNature aims for an ultimate size of 113,500 ha (Elbé Cloete, pers. comm. 2008).

The high diversity and endemism among plants of the Knersvlakte is attributed mainly to pronounced small-scale heterogeneity in abiotic soil characteristics (Schmiedel and Jürgens, 1999). Further, Desmet (2007) gives a short overview on different hypotheses on the drivers (e.g. habitat discontinuity, longer term climatic fluctuations) possibly involved in the evolution processes that are responsible for this high rate of endemism and diversity. However, the role of herbivory in evolutionary adaptation processes should not be underestimated (Desmet, 2007). The conservation area has been used for grazing of domestic livestock since about 2000–1600 years before present by Khoikhoi pastoralists practicing transhumant land use (Boonzaier et al., 2000) and more intensively during the last 150–200 years mainly by private farmers. Besides the presence of domestic animals (mainly sheep and goats), wild ungulates (e.g. antelopes, elephants and black rhinoceroses) used to roam the country but have been drastically reduced in numbers since the intensification of livestock farming (Hoffman and Rohde, 2007). Therefore, complete removal of domestic animals in the course of establishing a protected area might change

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the unique flora of the Knersvlakte by removing an important driver for the dynamics and the rejuvenation of the vegetation. However, heavy grazing has been shown to be one of the main causes for degradation and loss of biodiversity in arid and semi-arid environments (Cowling and Hilton-Taylor, 1994; Fleischner, 1994; West, 1993). Further, compositional shift, especially from a vegetation dominated by perennials to one dominated by annuals (Milton et al., 1994; Milton and Hoffman, 1994; Todd and Hoffman, 1999), as well as reduced seed numbers and germination rates (Riginos and Hoffman, 2003) have been reported as responses to overutilization.

To provide baseline data for decision making for future conservation management, a deeper understanding of the current effects of livestock on local vegetation composition and dynamics is required. The aim of this study was to examine the effects of current livestock grazing on the vegetation of the Knersvlakte in order to assist in decisions about appropriate future land use management. By comparing adjacent farms in the Knersvlakte that are subject to different grazing intensities the following research questions were addressed:

– Does grazing by domestic livestock affect plant communities of different habitat types in terms of species composition, life history and diversity, with particular respect to endemic taxa?
– Does grazing affect the seedling abundance in general or the reproduction of selected perennial plant species in particular?

2. Methods

2.1. Study area

The Knersvlakte (30°27′–32°05′S, 17°46′–19°06′E) is an extensive peneplain in the Western Cape province of South Africa. The altitude ranges from 50 to 600 m a.s.l. (van Wyk and Smith, 2001). The Knersvlakte comprises an area of 13,500 km^2 and forms the southernmost part of the Namaqualand, which belongs to the Succulent Karoo Biome (Milton et al., 1997; Rutherford and Westfall, 1994). According to Myers et al. (2000), the Succulent Karoo is the only arid region among the 25 internationally recognised biodiversity hotspots.

With more than 150 endemic vascular plant species (van Wyk and Smith, 2001), the Knersvlakte is often referred to as a centre of endemism and diversity (Jürgens, 1997; van Wyk and Smith, 2001), and is also known as the Vanrhynsdorp Centre (Hartmann, 1991; Hilton-Taylor, 1994; Nordenstam, 1969). The climate is characterised by a relatively predictable winter rainfall with an average of 116 mm per year (mainly falling in May–August), occasionally supplemented by fog and dew. Temperatures range from 5–10 °C in winter to 30–35 °C in summer (Mucina et al., 2006).

Also characteristic of the Knersvlakte is the frequent occurrence of quartz fields in which quartz gravel forms up to 100% ground-surface cover. The quartz gravel derived from weathered quartz veins running through parental material of limestone, shale and phyllites (Schmiedel and Jürgens, 1999). These conditions create a unique habitat with a distinct flora dominated by succulent compact dwarf chamaephytes, mainly Aizoaceae. The zonal matrix habitat types consist of sandy to loamy soils without quartz gravel cover, and are characterised by shrubby chamaephyte vegetation. These are henceforth referred to as 'non-quartz', while the quartz field habitats are henceforth referred to as 'quartz'.

2.2. Sampling design

Four farms with three different livestock (sheep, goats) grazing intensities located in the central prospective Knersvlakte Conservation Area were selected. The selected farms were Rooiberg and Hoogstaan as intensively grazed farms ('high'), Ratelgat as a moderately grazed ('moderate') and Quaggaskop as an ungrazed farm ('no') (Fig. 1, Table 1). They are situated 30–50 km north of Vanrhynsdorp and about 30 km east of the Atlantic Ocean.

Data were collected from early August to early November, 2007. Altogether, 51 plots (for GPS coordinates see El. App. A) were set up at homogenous sites representative of each farm. Grazing intensity (no, moderate, high) was represented by eight replicates on non-quartz and nine replicates on quartz habitats. Each plot was 20×50 m (0.1 ha) in size and contained 100 subplots. These measured 20×20 cm and were arranged in a regular grid (compare El. App. B).

For each subplot, the following parameters were recorded:

Microhabitat: The microhabitat of the subplot was determined using three categories of quartz cover density (high: >2/3; medium: 1/3–2/3; low: <1/3 cover).
Microtopography: The height difference between the lowest and highest point was measured and grouped into three categories (flat: <1 cm, medium: 1–5 cm; hilly: >5 cm).
Species: The identity and abundance of all vascular plant species rooting in the subplots were determined. Recognized taxonomic units that could not be assigned to described species were given field names or they were determined at a higher taxonomic level (see El. App. C). Nomenclature follows Germishuizen and Meyer (2003).
Developmental stage: All vascular plant individuals were classified into three age classes according to developmental stages of leaves and habit (seedling: only cotyledons developed; juvenile: additional leaves; adult: species-specific habit fully developed).
Number of reproductive structures: Individual flowers or inflorescences and fruits or fruit clusters of all individuals of chamaephytes and phanerophytes were counted.

2.3. Soil analysis

One mixed soil sample from 1 to 11 cm soil depth was collected on each plot (i.e. after removal of the top crust layer) and air dried. The soil was sieved (mesh wide: 2 mm) to prepare for subsequent analyses (conducted in the laboratory at the University of Hamburg, Germany).

We measured pH, conductivity and carbonate content of the soil, as previous studies showed that these parameters are the main drivers for plant species composition and vegetation structure in the study are (Schmiedel and Jürgens, 1999).

For pH measurement, a sub-sample of 10 g was suspended in 25 ml $CaCl_2$ (0.01 mol l^{-1}) for 1 h and then measured with a pH-meter (Schott CG837, electrode BlueLine 28 ph-P) for 5 min. The electrical conductivity was determined with an electrode (LF197, WTW) in a suspension of 10 g soil and 25 ml bidistilled water (van Reeuwijk, 1995). Carbonate content was estimated by a HCl test on a 7-point ordinal scale according to AG Boden (2005).

2.4. Data analyses

Inferential statistical analyses were conducted with STATISTICA 8.0 (StatSoft Inc., 2007). Normal distribution and homogeneity of variance were assessed visually as recommended by Quinn and Keough (2002). Data strongly deviating from normal distribution or with heterogenic variances were transformed using log transformation or non-parametric tests were used.

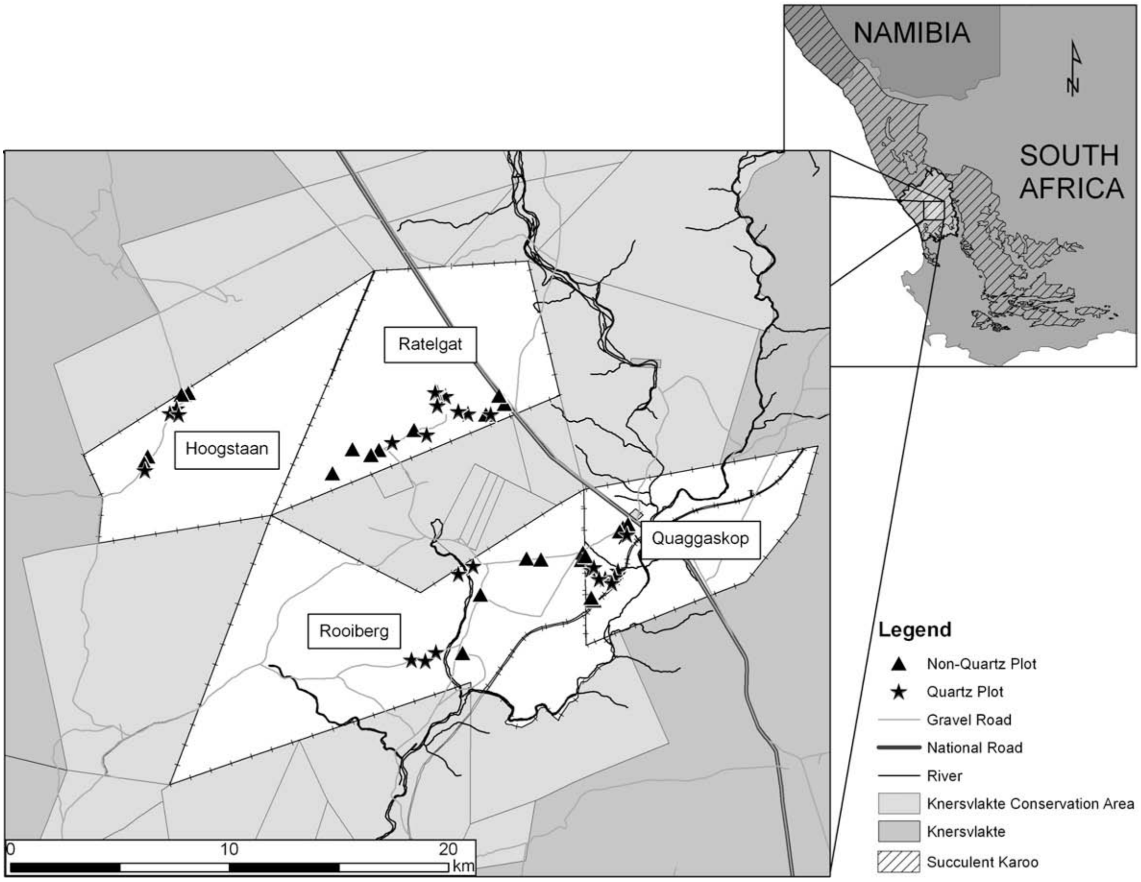

Fig. 1. Study area. Investigated farms are printed in white and labelled with their names (crossed lines = farm borders). Grazing intensities: Quaggaskop: no grazing; Ratelgat: moderate grazing; Hoogstaan and Rooiberg: intensive grazing. Shapefiles of farms, rivers and roads were kindly provided by CapeNature.

Table 1
Names and important characteristics of the farms investigated. SSU = small stock unit after Esler et al. (2006).

Farm name	Size (ha)	Grazing intensity	Ownership	Comments
Hoogstaan	6000	High (10 ha/SSU)	Private	Intensive grazing for the past about 50 years, interrupted by a 10 year-period of light grazing (1982–1992: 26 ha/SSU) Grazing regime: rotational herding between camps
Rooiberg	11,500	High (12 ha/SSU)	State land	Past 20 years: use of only about 7000 ha of the farmland by several informal settlers. 1984–1987: use of the farm for military training causing a high level of degradation Grazing regime: the sheep freely move in between a roughly defined area
Ratelgat	7000	Moderate (17 ha/SSU)	Private	Moderate grazing since 2000. Before that, only sporadic use for farming Grazing regime: rotational herding between camps.
Quaggaskop	5000	No	Private	The studied section (1500 ha) with no grazing for the past 40 years

2.4.1. Community level: diversity measures

For the analyses at community level, we used several parameters for abundance and diversity measurements. Plot data are represented by cumulative data of the one hundred 400-cm^2 subplots of the respective 0.1 ha plot. Seedlings were excluded from the statistical analyses of the parameters described in Table 2 due to identification difficulties.

To analyse differences between quartz and non-quartz habitats as well as between grazing intensities, we performed analyses of variance (ANOVAs) for each parameter as well as for pH and conductivity (Table 2). For differences in carbonate content, we performed a non-parametric Mann–Whitney *U* test since ranked data were used. Data with more than two categories were further analysed with the Tukey's HSD post hoc test (at $\alpha = 0.05$). To take into account potentially confounding effects of soil parameters on differences between grazing intensities, we performed Analyses of Covariance (ANCOVAs) with soil pH as well as with electrical conductivity as linear predictors.

2.4.2. Community level: species composition

To test the fidelity of the species to the units investigated (i.e. habitat type, grazing intensities), we determined ϕ coefficients (Chytrý et al., 2002) for all species in the different units. The ϕ coefficient is a measure of association between two categories (in this case species and investigated unit). It takes values from −1 to +1, with the latter indicating complete reciprocal fidelity of a species and a unit (Chytrý et al., 2002). ϕ-Values were grouped into four categories (Chytrý, 2007): $\phi \geqslant 0.50$: highly diagnostic, $0.25 \leqslant \phi < 0.50$: diagnostic; $0.00 \leqslant \phi < 0.25$: positively associated non-diagnostic; $\phi < 0.00$: negatively associated non-diagnostic. Fisher's exact test was used to test whether the association of a species with a unit was statistically significant (at $\alpha = 0.05$).

Table 2
Comparison of parameters 1–13 with description and environmental data for non-quartz and quartz plots (mean ± standard deviation or *median). In the right column the *p*-value for differences between the two habitat types is given (ANOVA; df = 49; *N* = 51 or **Mann–Whitney *U*-test). *p*-Values printed in bold indicate significant differences.

	Parameter	Description	Quartz	Non-quartz	*p*-Value
1	Total individuals	Number of individuals per plot	186 ± 116	330 ± 197	**0.002**
2	Individuals of endemic species	Number of individuals of Knersvlakte endemic species per plot (see also El. App. C)	75 ± 42	34 ± 12	**<0.001**[1]
3	Individuals of perennial species	Number of individuals of above-ground perennial species (i.e. chamaephytes and phanerophytes) per plot	123 ± 73	74 ± 18	**0.005**[1]
4	Individuals of annual species	Number of individuals of annual species	56 ± 72	237 ± 193	**<0.001**[1]
5	Plot species richness	Number of species per plot	23 ± 6	31 ± 6	**<0.001**
6	Mean species richness	Average number of species of all subplots per plot	1.14 ± 0.47	1.66 ± 0.62	**0.002**
7	Plot evenness	Shannon-evenness (E) of a plot's vegetation	0.46 ± 0.12	0.42 ± 0.17	0.335
8	Plot/subplot ratio	Ratio of plot species richness (see 5) and average number of species of all subplots (see 6) per plot. This is used as a measure of β-diversity (Whittaker, 1960)	22 ± 7	21 ± 6	0.439
9	Endemic species richness	Species richness per plot for endemic species described under 2	8 ± 3	6 ± 2	**0.013**
10	Endemic evenness	Shannon evenness E (see 7) per plot for local endemic species described under 2	0.58 ± 0.15	0.71 ± 0.12	**0.001**
11	Perennial species richness	Species richness of perennial species described under 3 per plot	15 ± 5	15 ± 3	0.874
12	Perennial evenness	Shannon evenness (see 7) per plot for species described under 3	0.49 ± 0.14	0.62 ± 0.11	**<0.001**
13	Annual species richness	Number of annual species per plot	6 ± 3	12 ± 3	**<0.001**
	pH		6.33 ± 1.31	7.67 ± 0.47	**<0.001**[1]
	Conductivity [$\mu S\ cm^{-1}$]		4836 ± 2405	2554 ± 2117	**<0.001**[1]
	Carbonate content (ordinal scale with range of 1–7)		1*	3*	**<0.001****

[1] Results for log transformed data.

2.4.3. Population level: reproduction

We conducted ANOVAs for each selected species to test for differences between grazing intensities with the geometric mean of reproductive structures per plot as the response variable. These analyses were carried out for perennial species (chamaephytes and phanerophytes, see El. App. D) that were unambiguously identified by species name or field name and were present as adults carrying reproductive structures on at least three plots of each grazing intensity.

For a combined analysis of all selected species, we standardised the species values by dividing the log-transformed numbers of the reproductive structures of each individual by the species' mean. We averaged the values for each species and conducted an ANOVA to test for differences between grazing intensities.

2.4.4. Population level: number of seedlings

For the analyses of the effects of grazing on the germination of seedlings, we analysed: (i) all seedlings, (ii) seedlings of the Aizoaceae, and (iii) all other seedlings. As the data were Poisson-distributed and log-transforming was impractical due to high numbers of zeros, we used the non-parametric Kruskal–Wallis-Test for the analyses of seedling numbers.

With the mean number of above mentioned seedling groups per subplot and plot we analysed differences between habitat types, grazing intensities, microhabitat (expressed as quartz cover) and microtopography on subplot level. For this we used Kruskal–Wallis-Tests with the mean seedling frequencies per subplot, category (in the latter two cases) and plot.

3. Results

3.1. General characterisation of the plots

In total, 173 taxonomic entities of vascular plants (further referred to as 'species' or 'taxa') were recorded with 16,563 individuals (10,343 adults, 2607 juveniles and 3613 seedlings). While 132 taxa could be clearly identified as described species, 15 were referred to unambiguously by field name (only two of them with unknown genus or family) and 20 taxa were determined at the family or genus level without unambiguous species identification. Six could not be attributed to specific families (see El. App. C). Taxa on intensively grazed ($n = 17$) and on ungrazed plots ($n = 17$) totalled 124 each, while we found 105 taxa on moderately grazed plots ($n = 17$). For an illustration of the ten most abundant species recorded on quartz and non-quartz plots and of the most abundant families, see El. App. E and F. The three most abundant species of each grazing intensity class and their percentage contribution are illustrated in El. App. G.

Of the 132 clearly identified species, 40 were endemic to the Knersvlakte, including 32 Aizoaceae species (see El. App. C). The prevailing life forms were chamaephytes and therophytes (see El. App. D).

3.2. Community level: biodiversity

3.2.1. Habitat types

The two habitat types, quartz and non-quartz, differed significantly in most of the tested biodiversity measures as well as in their soil properties (Table 2). Non-quartz plots had a higher total number of individuals and species, but lower numbers of endemic individuals and species. Non-quartz plots contained more annual but less perennial individuals than quartz plots. The species richness of annuals was higher in non-quartz plots than in quartz plots, but perennial species richness did not differ between the habitat types. Evenness of total species composition did not differ significantly, but evenness of endemic as well as of perennial species composition was higher in non-quartz than in quartz plots. The quartz plots had lower and more varying soil pH values and higher conductivity than the non-quartz plots. Carbonate content was higher in non-quartz soils.

3.2.2. Grazing intensities

As habitat types differed in most of the tested parameters (compare Section 3.2.1), we conducted the following analyses separately for quartz and non-quartz plots. See Table 3 for a complete list of the results.

3.2.2.1. Non-quartz plots. The number of individuals, annual individuals as well as the mean species richness in non-quartz plots was significantly lower in moderately grazed than in ungrazed

Table 3
Summary of the ANOVA and ANCOVA results for the parameters 1–13 for differences between grazing intensities for non-quartz (left) and quartz (right) plots and their means ± SD. *p*-Values printed in bold indicate significant differences; different superscript letters indicate significant differences according to Tukey's test.

		Quartz ($N = 27$)						Non-quartz ($N = 24$)					
		No (mean ± SD) $n = 9$	Moderate (mean ± SD) $n = 9$	High (mean ± SD) $n = 9$	*p*-Value ANOVA	*p*-Value ANCOVA (pH)	*p*-Value ANCOVA (conductivity)	No (mean ± SD) $n = 8$	Moderate (mean ± SD) $n = 8$	High (mean ± SD) $n = 8$	*p*-Value ANOVA	*p*-Value ANCOVA (pH)	*p*-Value ANCOVA (conductivity)
1	Total individuals	279 ± 108^{a}	118 ± 51^{b}	162 ± 117^{b}	**<0.001**[1]	**0.009**	0.172	425 ± 123^{a}	171 ± 64^{b}	394 ± 254^{a}	**0.001**	**0.002**	**0.002**
2	Individuals of endemic species	100 ± 42^{a}	73 ± 38^{ab}	52 ± 33^{b}	**0.041**	**0.036**	0.170	29 ± 14	35 ± 8	37 ± 14	0.443	0.443	0.29
3	Individuals of perennial species	187 ± 82^{a}	105 ± 46^{b}	78 ± 36^{b}	**0.001**	**0.001**	**0.028**	81 ± 25	69 ± 14	73 ± 15	0.512	0.643	0.794
4	Individuals of annual species	89 ± 48^{a}	11 ± 9^{b}	68 ± 105^{ab}	**0.012**	**0.048**	**0.045**	321 ± 125^{a}	93 ± 66^{b}	296 ± 258^{a}	**0.003**	**0.004**	**0.005**
5	Plot species richness	26 ± 6	21 ± 6	22 ± 7	0.282	0.383	0.164	35 ± 7	29 ± 4	29 ± 3	0.061	0.08	0.101
6	Mean species richness	1.51 ± 0.41^{a}	0.92 ± 0.30^{b}	1 ± 0.47^{b}	**0.009**	**0.017**	0.225	2.07 ± 0.63^{a}	1.12 ± 0.21^{b}	1.78 ± 0.52^{a}	**0.001**	**0.001**	**0.002**
7	Plot evenness	0.41 ± 0.10	0.51 ± 0.11	0.46 ± 0.14	0.190	0.470	0.666	0.32 ± 0.13^{a}	0.55 ± 0.12^{b}	0.39 ± 0.18^{ab}	**0.016**	**0.012**	**0.025**
8	Plot/subplot ratio	18 ± 5	24 ± 7	24 ± 8	0.086	0.059	0.811	17 ± 4^{a}	27 ± 5^{b}	17 ± 5^{a}	**<0.001**	**<0.001**	**0.001**
9	Endemic species richness	9 ± 3	9 ± 3	6 ± 3	0.177	0.233	0.109	7 ± 2	7 ± 1	5 ± 2	0.096	0.102	0.099
10	Endemic evenness	0.56 ± 0.12	0.54 ± 0.14	0.63 ± 0.19	0.438	0.348	0.446	0.78 ± 0.11	0.66 ± 0.16	0.71 ± 0.07	0.16	0.158	0.145
11	Perennial species richness	16 ± 4	17 ± 5	14 ± 7	0.451	0.639	0.324	16 ± 2^{ab}	17 ± 3^{a}	13 ± 2^{b}	**0.014**	**0.017**	**0.012**
12	Perennial evenness	0.41 ± 0.13	0.51 ± 0.11	0.55 ± 0.14	0.073	0.085	0.280	0.61 ± 0.09	0.64 ± 0.11	0.61 ± 0.13	0.762	0.817	0.794
13	Annual species richness	8 ± 2^{a}	4 ± 2^{b}	5 ± 3^{b}	**0.001**	**0.008**	**0.012**	14 ± 4^{a}	10 ± 2^{b}	12 ± 3^{ab}	**0.043**	0.06	0.071

[1] Results of log transformed data.

and intensively grazed plots. Plot evenness, however, was highest in moderately grazed plots and lowest in ungrazed plots. Similarly, the plot/subplot ratio of species richness was highest in moderately grazed plots and significantly lower in ungrazed as well as in intensively grazed plots. Plot species richness was insignificantly higher in ungrazed compared to grazed plots. Perennial species richness was highest in moderately grazed plots and lowest in intensively grazed plots. Ungrazed plots contained the highest and moderately grazed plots the lowest number of annual species. This result became insignificant when including pH or conductivity as covariates in an ANCOVA.

3.2.2.2. Quartz plots. Only the number of perennial and annual species as well as the annual species richness showed significant differences in the ANOVA and both ANCOVAs. Ungrazed plots contained the highest number of annual and perennial individuals as well as annual species.

The following parameters differed significantly for ANOVAs as well as ANCOVAs with pH as a covariate but not for ANCOVAs with conductivity as a covariate. Ungrazed sites contained significantly more individuals and had higher mean species richness than moderately as well as intensively grazed sites. The number of individuals of endemic taxa was highest on ungrazed plots and lowest on intensively grazed plots with significant differences between the ungrazed and intensively grazed plots.

3.3. Community level: species composition

In quartz plots, 17 species (11 endemics among them) were significantly associated and 29 (four endemics) in non-quartz plots (compare El. App. C). According to ϕ-values, only one species (*Drosanthemum schoenlandianum*, an endemic) was highly diagnostic for non-quartz plots and none for quartz plots. The species highly diagnostic and significantly associated for the three grazing categories are illustrated in Table 4 with special reference to endemic species.

3.4. Population level: reproduction

In total, seven perennial species were present as individuals carrying reproductive structures in at least three plots per grazing intensity level and were thus included in the reproduction assessment.

Table 4
Species that were significantly associated at one of the three grazing intensities (quartz and non-quartz separately) according to Fisher's exact test. C = chamaephyte, G = geophyte, T = therophyte; endemic species are printed in bold; *highly diagnostic species according to ϕ-values (see also El. App. C).

Grazing intensity	Quartz	Life form type	Non-quartz	Life form type
No	***Argyroderma delaetii****	C	*Crotalaria meyeriana*	C
	Cephalophyllum framesii	C	*Gazania lichtensteinii*	T
	*Crotalaria meyeriana**	C	*Lachenalia framesii**	G
	Mesembryanthemum guerichianum	T	*Senecio abruptus*	T
	*Mesembryanthemum longistylum**	T	*Senecio arenarius*	T
	Oophytum nanum	C		
	*Senecio arenarius**	T		
Moderate	***Antimima watermeyeri****	C	***Antimima solida****	C
	Tetragonia fruticosa	C	*Crassula expansa* ssp. *pyrifolia**	C
	Ursinia nana	T	*Othonna protecta*	C
			Ruschia bolusiae	C
High	*Gazania lichtensteinii*	T	*Galenia sarcophylla*	C
	*Sarcocornia xerophila**	C		

Table 5
Mean numbers (±SD) of seedlings per subplot for the habitat types, grazing, microhabitat and microtopography categories and results of the Kruskal–Wallis-Test. *p*-Values printed in bold indicate significant differences; different letters in superscripts indicate significant differences among levels.

Habitat	Quartz (mean ± SD) $n = 27$	Non-quartz (mean ± SD) $n = 24$		*p*-Value
Number of seedlings	0.82 ± 0.79	0.57 ± 0.63		0.390
Number of Aizoaceae seedlings	0.68 ± 0.67	0.29 ± 0.23		0.055
Number of non-Aizoaceae seedlings	0.14 ± 0.32	0.26 ± 0.48		0.264
Grazing intensities	No (mean ± SD) $n = 17$	Moderate (mean ± SD) $n = 17$	High (mean ± SD) $n = 17$	*p*-Value
Number of seedlings	0.84 ± 0.70	0.43 ± 0.42	0.83 ± 0.93	0.193
Number of Aizoaceae seedlings	0.69 ± 0.64	0.31 ± 0.34	0.48 ± 0.56	0.129
Quartz: number of Aizoaceae seedlings	1.08 ± 0.65^{a}	0.31 ± 0.43^{b}	0.64 ± 0.71^{ab}	**0.017**
Non-quartz: number of Aizoaceae seedlings	0.26 ± 0.24	0.32 ± 0.23	0.30 ± 0.26	0.820
Number of non-Aizoaceae seedlings	0.15 ± 0.27	0.10 ± 0.16	0.34 ± 0.61	0.972
Microhabitat (quartz cover)	Low (mean ± SD) $n = 46$	Medium (mean ± SD) $n = 39$	High (mean ± SD) $n = 30$	*p*-Value
Number of seedlings	0.46 ± 0.57^{ab}	0.34 ± 0.58^{a}	0.87 ± 0.98^{b}	**0.013**
Number of Aizoaceae seedlings	0.26 ± 0.32^{a}	0.21 ± 0.39^{a}	0.74 ± 0.85^{b}	**<0.001**
Number of non-Aizoaceae seedlings	0.18 ± 0.40	0.13 ± 0.32	0.13 ± 0.31	0.642
Microtopography	Flat (mean ± SD) $n = 51$	Medium (mean ± SD) $n = 51$	Hilly (mean ± SD) $n = 43$	*p*-Value
Number of seedlings	0.77 ± 0.79^{a}	0.53 ± 0.65^{ab}	0.53 ± 0.80^{b}	**0.007**
Number of Aizoaceae seedlings	0.57 ± 0.61^{a}	0.32 ± 0.38^{a}	0.29 ± 0.53^{b}	**<0.001**
Number of non-Aizoaceae seedlings	0.19 ± 0.39	0.21 ± 0.44	0.24 ± 0.51	0.355

Individuals of both *Argyroderma fissum* and *D. schoenlandianum* had the highest number of reproductive structures in moderately grazed plots *D. diversifolium*, *D.* spec. 1 ('glossy') and *Malephora purpureo-crocea* showed the same trend, though insignificantly (El. App. H).

The combined analysis over all investigated species confirmed this trend of highest numbers in moderately grazed plots. The difference between the grazing intensities was marginally significant with $p = 0.050$.

3.5. Population level: number of seedlings

The two habitat types differed with marginal significance in abundance of Aizoaceae seedlings per subplot (averaged per plot): in quartz plots more than twice as many Aizoaceae seedlings occurred as in non-quartz plots. The total numbers of seedlings and the numbers of non-Aizoaceae seedlings did not differ between habitat types (Table 5).

When quartz and non-quartz plots were combined, the results for the three grazing intensities differed neither in total number of seedlings nor when differentiating between Aizoaceae and non-Aizoaceae seedlings. When only the quartz plots were taken into account, the numbers of Aizoaceae seedlings differed significantly between grazing intensities. The highest number of seedlings occurred in ungrazed and the lowest in moderately grazed plots (Table 5).

The three microhabitat categories of quartz cover densities differed significantly in their total numbers of seedlings and highly significantly in their numbers of Aizoaceae seedlings. No differences in the numbers of non-Aizoaceae seedlings could be detected between the categories of quartz cover densities (Table 5).

The three microtopography categories differed significantly in their numbers of Aizoaceae seedlings, with the highest number of seedlings encountered on flat surfaces (i.e. relief less than 1 cm, see Table 5).

4. Discussion

4.1. Effects of grazing at the community level

4.1.1. Abundance of plant individuals and life history types

The abundance of plant individuals showed different patterns for quartz and non-quartz plots. However, both habitat types showed significant variances for total individuals, which was, on non-quartz plots, mainly driven by the abundance of annual individuals. Among the non-quartz plots ungrazed and intensively grazed sites had high numbers of individuals due to high abundance of annuals.

In contrast, the abundance pattern in quartz plots was determined by perennials and annuals, both of which were most abundant in ungrazed plots. Since the most abundant species in ungrazed and moderately grazed plots were endemic chamaephytes and, additionally, the number of endemic individuals was lowest in intensively grazed plots, high grazing intensity seems to have a particularly negative impact on endemic species.

As the abundance of annuals did not significantly increase with grazing intensity in quartz or in non-quartz plots and was even lowest on the moderately grazed farm Ratelgat, the shift in species composition from perennial towards annual species in response to grazing pressure described for the Succulent Karoo (Desmet, 2007; Milton and Hoffman, 1994; Todd and Hoffman, 1999) and for other biomes (Grime, 2001; West, 1993) was not found. However, quartz fields showed other signs of vegetation change due to grazing: total abundance of individuals, abundance of individuals of endemic as well as perennial species decreased significantly compared to no grazing.

The generally low abundance of annuals under moderate grazing could be explained by factors other than grazing such as spatially differing rainfall patterns or soil properties such as water storage capacity or nutrient availability (Gillson and Hoffman, 2007). Anderson and Hoffman (2007) as well as Hendricks et al. (2005) argued that precipitation was the most likely cause for the abundance of annuals on heavily grazed sites in the Succulent Karoo. The increased cover of annuals due to grazing pressure in a fence line contrast study in the Kamiesberg area of the upland Succulent Karoo described by Todd and Hoffman (1999) can also be ascribed to the high precipitation in the year of data collection. As the moderately grazed farm showed generally low abundance of individuals of annual species as well as low richness of annual species, it can be assumed that this farm received less rainfall in the year of investigation than the other farms investigated in this study, although such a spatially heterogeneous rainfall pattern would be rather unusual for the winter rainfall region of southern Africa (Desmet, 2007). However, this suggestion is supported by the comparison of data from a weather station on the moderately grazed farm Ratelgat with those from another one on a farm 25 km south-west (Moedverloren). During the preceding wet season (April–August) Ratelgat received 41% less rain than Moedverloren (BIOTA AFRICA, unpublished data).

4.1.2. Plant diversity

On non-quartz fields, the moderately grazed plots contained the lowest number of species per subplot (400 cm^2). This would suggest a negative effect of moderate grazing but not of intensive grazing on species richness, which is contrary to most other studies (Ayyad and Elkadi, 1982; Eccard et al., 2000; Naveh and Whittaker, 1979; Olsvig-Whittaker et al., 1993) and to the intermediate disturbance hypothesis (Connell, 1978; Grime, 1973). This, as well as the highest β-diversity and evenness on moderately grazed plots, can be explained by the very low number of therophytes on moderately grazed plots in comparison to the other grazing intensities. The majority of therophyte species in the study area belongs to the Asteraceae and are wind-dispersed, opportunistic and typically occur in high abundances. This has a homogenising effect on the vegetation. In contrast, the majority of the perennial species belong to the Aizoaceae which are habitat specific and characterised by ombrohydrochorous (dispersed by rain) short-distance dispersal (Parolin, 2006). This is an important factor responsible for the patchy, heterogeneous distribution of the Aizoaceae (compare also Desmet and Cowling, 1999; Schmiedel and Jürgens, 1999). Differences in abundance of annual and perennial species can thus have an effect on the β-diversity and evenness of the Knersvlakte vegetation.

In quartz fields, in contrast to non-quartz fields, the ungrazed plots contained the highest average number of species per subplot as well as the highest total plant species richness at the plot level (insignificant trend). Moreover, the number of annual species was highest on ungrazed plots. No grazing with only low level, localised disturbance by burrowing small mammals would provide the intermediate disturbance which may support highest levels of diversity as predicted by Grime (1973) and Connell (1978). Any increase of disturbance due to grazing of livestock has a negative impact on species diversity. The low negative impact threshold of disturbance can be explained by the very low productivity of the quartz fields, which is due to their extreme habitat conditions (Schmiedel and Jürgens, 1999). In particular, the abundance of annuals on quartz fields decreases even under moderate grazing. This can be attributed to the fact that the annuals, mainly Asteraceae species, are much more palatable to stock than the perennial quartz field species, which are mainly Aizoaceae species (Schmiedel, unpublished observations). The latter typically remain ungrazed (except for the flowers during anthesis), but suffer from trampling of roaming livestock.

4.1.3. Species composition

The results regarding the highly diagnostic and significantly associated species indicate a much higher floristic variability among quartz plots than among non-quartz plots. They also indicate strong differences in species composition between the different grazing intensities on quartz fields. This is in concordance with Schmiedel (2002), who identified 67 obligate quartz field species for the entire Knersvlakte. Only four of them are widespread in the Knersvlakte whereas the other species were recorded only from parts of the area.

The ungrazed farm Quaggaskop and the moderately grazed farm Ratelgat host a number of locally endemic habitat specialists, in both quartz and non-quartz plots. The few significantly associated and highly diagnostic species on the intensively grazed farms were not endemic to the Knersvlakte. This gives both the farms Quaggaskop (no grazing) and Ratelgat (moderate grazing) and their grazing regimes a higher conservation significance and substantiates the hypothesis of a floristic homogenisation of heavily grazed rangeland (Ludwig and Tongway, 2000).

For a deeper understanding of the processes underlying compositional shifts in response to grazing as well as for estimating the extent to which specific plant communities are impacted by grazing, studies about food preferences and palatability of plant species in this region are essential (like the study by Hendricks et al. (2002) in the Richtersveld National Park).

4.1.4. Role of environmental parameters

In non-quartz plots, the recorded environmental parameters did not significantly alter the results regarding the impact of grazing when used as covariates in the ANCOVAs. This suggests that the effects found for non-quartz plots were due to grazing alone and not biased by the measured soil properties. Nevertheless, this does not exclude possible effects of other parameters, such as small-scale rainfall patterns (which seemed to have had an effect on some of the results of this study), spatial distance (Bertram, 2006; Parolin, 2006), micro-climate (Schmiedel and Jürgens, 2004), or other soil properties, such as soil moisture, texture or stone content (Ellis and Weis, 2006).

In quartz plots, the measured soil properties showed an effect on the diversity, abundance and species composition. These results are in line with Schmiedel and Jürgens (1999) and Schmiedel (2002). While species abundance and diversity of the quartz plots were not influenced by soil pH, soil salinity (electrical conductivity) did affect mean species richness and the abundance of all species and the endemic species. This indicates a high importance of soil salinity for abundance and diversity patterns of species on quartz plots and might overweigh the effects of grazing pressure. As salinity amplifies the effects of drought by lowering the osmotic potential in the soil (Campbell and Reece, 2005), it can be assumed that the abundance and diversity of plant species on quartz fields is mainly determined by soil water availability, exacerbated by salinity.

4.2. Effects of grazing at the population level

4.2.1. Reproduction

The production of flowers and fruits increased under moderate but not intensive grazing in two of the seven studied species, namely *A. fissum* and *D. schoenlandianum*. A combined analysis across all seven species showed the same trend. An explanation for this increase could be that injuries caused by moderate grazing or trampling stimulate the production of flowers which may overcompensate for the injuries by producing even more flowers (McNaughton, 1983). This mechanism has been demonstrated for other African species, for example the dwarf shrub *Indigofera spinosa* (Oba et al., 2000) and *Acacia drepanolobium* (Gadd et al., 2001), and could also apply for *D. schoenlandianum* which seems to be a palatable species, as its seeds were very frequently found in dung (Haarmeyer et al., in press). However, with a further increase of grazing pressure, the increased production of flowers might be insufficient to compensate for the trampling injuries and can thus be a major threat to fruit production as identified for the upland Succulent Karoo (Pufal et al., 2008). Also, Todd and Hoffman (1999) as well as Milton (1994) found a significant decrease in flowering or seed set in response to heavy grazing in two different palatable plant species, whereas an unpalatable species was not affected in the latter study.

A. fissum, the second species for which an increase in reproductive structures under moderate grazing has been found, is unpalatable to stock except for the flowers (Schmiedel, pers. obs.), and there was no indication in the field that this plant was grazed at all. Thus, it is unlikely that the detected increase of flowers of this species is related to grazing. Considering the likewise higher volume of *A. fissum* individuals on the moderately grazed farm Ratelgat, a more likely explanation is that the plants grow better on this farm in response to more suitable habitat conditions and therefore carry more flowers and fruits. Such small-scale adaptations to edaphic microenvironment have been shown for *Argyroderma* species by Ellis and Weis (2006). As not all species showed an increase of reproductive structures under moderate grazing pressure, it is likely that responses to grazing are species-specific.

4.2.2. Number of seedlings

The number of seedlings generally tended to be lowest on the moderately grazed farm. This is in line with the relatively low abundance of therophytes on the same sites and underpins the assumption of spatially differing precipitation patterns as discussed above. Based on these results it can be assumed that grazing and trampling may have a weaker effect on seedling numbers than other environmental drivers like rainfall. Milton (1994) also did not find an effect of grazing on seedling numbers during a study in the Great Karoo. In contrast, a study in the upland Succulent Karoo showed that heavy grazing may have a negative impact on recruitment of *Ruschia robusta* and *Cheridopsis denticulata*, two Aizoaceae species, due to limited seed numbers (Riginos and Hoffman, 2003). The findings suggest that only very intensive grazing affects germination and abundance of seedlings. The grazing intensities investigated in the Knersvlakte, even on the farms with relatively intensive grazing, were apparently not high enough to impair seedling recruitment.

The presence of quartz cover had a highly significant positive effect on the total number of seedlings found per subplot, which is mainly due to the contribution of Aizoaceae seedlings. This is in concordance with the higher abundance of Aizoaceae seedlings recorded in quartz plots than in non-quartz plots at the plot level (0.1 ha) and suggests a strong influence of quartz cover on recruitment of Aizoaceae seedlings. The soil between the quartz stones is less exposed to solar radiation and is therefore generally cooler (Schmiedel and Jürgens, 2004) and moister (Charles Musil, unpublished data) than the soil without quartz cover. As water uptake is essential for germination, the quartz habitat seems to better fulfil germination requirements for Aizoaceae seedlings than the non-quartz habitat.

Small depressions in the surface (generated, for instance, by sheep footprints) can act as seed and water traps. One could therefore expect an accumulation of seedlings on surfaces with more pronounced microtopography. This expectation was not met, as the number of seedlings was not higher on rougher surfaces. Aizoaceae seedlings were even recorded most frequently on soil surfaces classified as smooth. However, the measured effect could have been biased by other factors such as quartz cover, which also provides a certain roughness of the surface even though the soil surface itself appears to be smooth.

4.3. Conclusions and implications for nature conservation

The study revealed that the vegetation of the Knersvlakte is a complex system affected by multiple factors, where different vegetation parameters showed different responses to grazing pressure. The abundance, diversity and composition of species as well as reproduction and growth of some frequently occurring perennial species were only secondarily affected by grazing. Although overgrazing is by all means a serious problem by promoting degradation processes and should certainly not be encouraged, the main drivers of vegetation and population dynamics in the Knersvlakte seem to be small-scale patterns in soil properties (quartz cover, salinity). Additionally, variation in rainfall patterns also seems to contribute to spatial differences which, however, would only have temporary effects.

Despite its minor role, grazing showed effects on some parameters (e.g. species abundance on quartz plots, number of diagnostic species and production of flowers in *D. schoenlandianum*). From a conservation perspective, no or moderate grazing appear to be necessary to preserve plant diversity vegetation patterns, and their underlying processes as both systems hosted unique locally endemic habitat specialists. Therefore, neither a complete ban nor an overall homogenous application of grazing is advisable when aiming to conserve the existing vegetation pattern with its unique flora and high endemism. Conservation-motivated management should consequently consider implementing both the exclusion of domestic livestock on some and the maintenance of controlled, moderate grazing intensity on other parts of the conservation area which are dominated by non-quartz soils. Limited grazing would also serve the growing interest in farm land by previously disadvantaged communities. Further studies should aim at evaluating whether the effects of moderate domestic livestock grazing can also be achieved by indigenous grazing animals. Additionally, studies on palatability and food preferences are needed to explore the effects of grazing on specific species or plant communities.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.11.008.

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