The impact of livestock grazing on plant diversity: an analysis across dryland ecosystems and scales in southern Africa

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Abstract. A general understanding of grazing effects on plant diversity in drylands is still missing, despite an extensive theoretical background. Cross-biome syntheses are hindered by the fact that the outcomes of disturbance studies are strongly affected by the choice of diversity measures, and the spatial and temporal scales of measurements. The aim of this study is to overcome these weaknesses by applying a wide range of diversity measures to a data set derived from identical sampling in three distinct ecosystems. We analyzed three fence-line contrasts (heavier vs. lighter grazing intensity), representing different degrees of aridity (from arid to semiarid) and precipitation regimes (summer rain vs. winter rain) in southern Africa. We tested the impact of grazing intensity on multiple aspects of plant diversity (species and functional group level, richness and evenness components, alpha and beta diversity, and composition) at two spatial scales, and for both 5-yr means and interannual variability. Heavier grazing reduced total plant cover and substantially altered the species and functional composition at all sites. However, a significant decrease in species alpha diversity was detected at only one of the three sites. By contrast, alpha diversity of plant functional groups responded consistently across ecosystems and scales, with a significant decrease at heavier grazing intensity. The cover-based measures of functional group diversity responded more sensitively and more consistently than functional group richness. Beta diversity of species and functional types increased under heavier grazing, showing that at larger scales, the heterogeneity of the community composition and the functional structure were increased. Heavier grazing mostly increased interannual variability of alpha diversity, while effects on beta diversity and cover were inconsistent. Our results suggest that species diversity alone may not adequately reflect the shifts in vegetation structure that occur in response to increased grazing intensity in the dryland biomes of southern Africa. Compositional and structural changes of the vegetation are better reflected by trait-based diversity measures. In particular, measures of plant functional diversity that include evenness represent a promising tool to detect and quantify disturbance effects on ecosystems.

Key words: alpha diversity; beta diversity; biodiversity; disturbance; evenness; fence-line contrast; functional diversity; Nama Karoo; rangeland degradation; richness; stability; Succulent Karoo.

INTRODUCTION

Land use has strongly influenced vegetation cover and diversity patterns of ecological communities in many parts of the world. In semiarid and arid ecosystems, and specifically in savannas, unsustainable livestock farming

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is considered the biggest driver of land degradation, which is defined as a decrease in productivity (Adeel et al. 2005), and loss of biodiversity (Sala et al. 2000). The effects of livestock grazing on biodiversity have been addressed by numerous studies. According to the intermediate disturbance hypothesis (IDH; Grime 1973, Connell 1978), plant diversity should be highest at intermediate levels of grazing intensity. The dynamic equilibrium model (DEM; Huston 1979, Kondoh 2001) then suggested that moderate grazing intensity should have positive effects on diversity in high-productivity systems and negative effects in low-productivity systems. This conceptual model received a further refinement by Milchunas et al. (1988) who added, as a third variable, the evolutionary history of grazing in the respective region. Consequently, their model predicted that the longer a certain ecosystem was exposed to grazing

pressure in evolutionary time, the weaker the reaction to grazing should be.

However, despite these extensive conceptual frameworks, we still lack a general understanding of how grazing affects biodiversity in rangelands. Empirical studies have revealed inconsistent responses of plant species diversity to grazing intensity: increasing, unimodal, decreasing, and no response (see reviews by Olff and Ritchie 1998, Mackey and Currie 2001, Cingolani et al. 2005). All these response shapes are theoretically compatible with the IDH or its later refinements, as the grazing intensity axis in these conceptual models does not have an unequivocal scaling (Svensson et al. 2009). In addition, there are a multitude of different measures of diversity (see Magurran and McGill 2011), and they can be applied at different spatial and temporal scales. Thus, it is important to recognize that outcomes of disturbance studies are affected by the choice of diversity measures and scaling laws (Mackey and Currie 2001).

Studies that encompass different diversity measures (e.g., Haarmeyer et al. 2010, Carmona et al. 2012) or different spatial scales (e.g., de Bello et al. 2007, Golodets et al. 2011), or which apply the same diversity measure across long geographic or climatic gradients (e.g., Bakker et al. 2006, Lavorel et al. 2011, Rutherford et al. 2012) are rather scarce in the scientific literature. In their seminal paper on grazing effects on plant community structure, Milchunas et al. (1988) presented diversity as a response variable without further specification. However, recent theoretical and empirical studies have demonstrated that different aspects of diversity often show varying, or even opposite responses to disturbance (Mouillot et al. 2013). There are four methodological aspects, where the choice of method may have important effects on the study outcomes of grazing (disturbance) effects on biodiversity.

First, diversity can be expressed by many different indices that represent richness, evenness, or a combination of both (Maurer and McGill 2011). In a meta-analysis of empirical IDH studies, Svensson et al. (2012) found dissimilar responses to disturbance in 75% of cases, when richness and evenness were compared. Furthermore, a simulation model resulted in a unimodal disturbance response of richness, while evenness showed a monotonic increase (Svensson et al. 2012). Also, for grazing as the disturbance, divergent responses of richness and evenness have been found in various studies (e.g., Haarmeyer et al. 2010, Rutherford and Powrie 2010, Golodets et al. 2011).

Second, while in the past, the relationship between diversity and grazing or other disturbances has been assessed mainly at the level of species (i.e., taxonomic diversity), there is now a growing awareness that functional diversity should be included in such studies, especially as it has been found to be more strongly related to ecosystem processes (Díaz and Cabido 2001, Petchey and Gaston 2006). Recent rangeland studies in the Mediterranean region suggest that the reorganization of the community structure in response to the selective pressure of grazing is well-reflected by measures of functional diversity (de Bello et al. 2006, Papanikolaou et al. 2011, Carmona et al. 2012). In most other arid and semiarid ecosystems, the quantification of land use effects on diversity has been limited to the species level, although there is a broad agreement that grazing alters the functional structure of the vegetation (e.g., Asner et al. 2004, Díaz et al. 2007, Rutherford et al. 2012).

Third, there is a broad consensus that factors shaping diversity patterns vary across spatial scales (Shmida and Wilson 1985, Siefert et al. 2012), an aspect only rarely addressed in grazing studies. According to the conceptual model of Olff and Ritchie (1998), grazing should increase plant species richness at smaller grain sizes and decrease it at larger grain sizes. Interestingly, one comparative study along a steep climatic gradient found that grazed grasslands were richer than ungrazed ones at all spatial scales under moist conditions, while in the semiarid part of the gradient the opposite was true (de Bello et al. 2007). Another way to look at scale-dependency is to apply measures of beta diversity, which describe how diversity changes with scale (Jurasinski et al. 2009, Jost et al. 2011). De Bello et al. (2007) demonstrated that, depending on the position along a climatic gradient from arid to humid conditions, species beta diversity reacted in a positive, unimodal, or negative way to grazing intensity.

Fourth, grazing effects on plant diversity are considerably influenced by temporal scales of measurement (Olff and Ritchie 1998), particularly in arid and semiarid ecosystems (Osem et al. 2002). Due to the high interannual rainfall variability in these systems, results of one-time assessments may be strongly biased by year-specific responses of plant populations (Jürgens et al. 1999, Wesuls et al. 2012). It is largely unknown how the response of biodiversity to interannual variability in abiotic conditions is modified by different levels of grazing pressure (but see Sternberg et al. 2000).

In our study conducted in the dryland biomes of southern Africa, we address several of the shortcomings of many previous studies on grazing effects on vascular plant diversity. We do so by (1) applying identical sampling in three different ecosystems, (2) analyzing data collected during five years instead of during a single year, (3) testing various aspects of biodiversity (richness and evenness components, alpha and beta diversity, different grain sizes, and composition), (4) comparing the response of species diversity and functional group diversity, and (5) analyzing both 5-yr means of all parameters and their interannual variability. The study is based on fence-line contrasts in three ecosystems differing in terms of aridity (from arid to semiarid conditions) and precipitation regimes (summer rain vs. winter rain). The fence-line contrasts result from decades of contrasting grazing intensity in immediately adjacent and abiotically very similar areas (Jürgens et al. 2010).
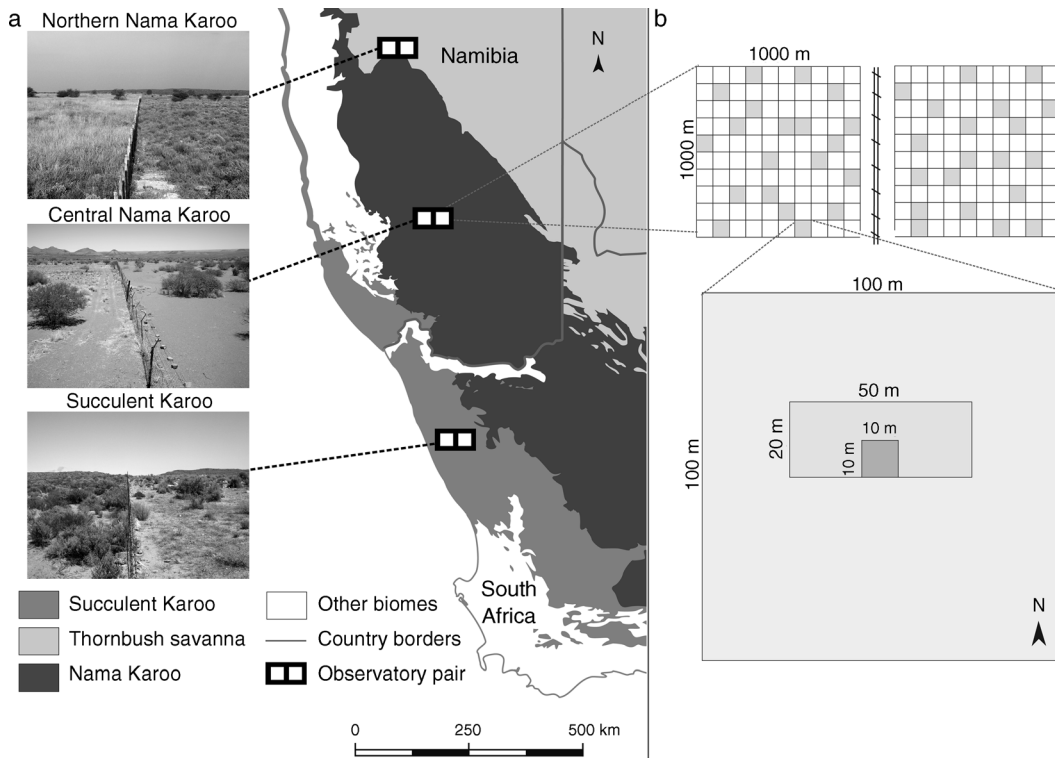
Fig. 1. (a) Location of our study sites within southwestern Africa and photographs of the fence-line contrasts (more lightly grazed observatories on the left and more heavily grazed observatories on the right sides of the fences), and (b) sampling scheme of an observatory, with 16–20 randomly selected 1-ha plots containing a nested 1000-m^2 and 100-m^2 plot each, modified after Jürgens et al. (2010).

Overall, our approach aims to gain a more generic understanding of the effects of grazing intensity on common measures used to quantify plant diversity, and to provide better-founded indicators for environmental conservation and sustainable management.

In particular, we address the following research questions: First, how do different components of plant diversity respond to grazing intensity at different spatial scales in different arid/semiarid ecosystems? Second, which changes in the composition of species and plant functional groups underlie the response of diversity? Third, which diversity aspects and measures are most sensitive for detecting and quantifying grazing effects on plant communities?

METHODS

Study sites

The study was conducted in three sites located in two major dryland biomes of southern Africa: the Nama Karoo and the Succulent Karoo. The three sites represent different climatic conditions from arid to semiarid, and from summer to winter rainfall regimes (Fig. 1a, Table 1). At each site, a pair of immediately adjacent BIOTA (biodiversity monitoring transect analysis in Africa) observatories with contrasting grazing regimes were established in 2001 (Jürgens et al.

2012). One observatory had been exposed to heavier grazing (actual stocking rate exceeds recommended stocking rate; no strict rotation of livestock), and the other to lighter grazing (stocking rate is below recommended stocking rate; strict rotation) for at least two decades (Table 1). We categorized the contrasting grazing regimes into the single factor grazing intensity (i.e., heavier vs. lighter) that combines stocking rate (above vs. below official recommendation) and management system (continuous vs. rotational). Since grazing intensity and management systems in the region do not occur independently of each other (i.e., heavier grazing nearly always goes along with continuous grazing and lighter grazing with rotational grazing), it would neither be sensible to study these two factors independent of each other (i.e., in a factorial design) nor possible in practice (at least not at landscape scale). This is the reason why other studies often employ a compound parameter, especially in cases where grazing effects are studied on a larger scale (e.g., Rutherford et al. 2012).

All three observatory pairs showed similar gradients in grazing intensity, with the actual stocking rates being approximately two times lower on the lighter than on the more heavily grazed observatory (Table 1). The contrasting grazing regimes resulted in fence-line contrasts with marked differences in structure and composition of the vegetation (Fig. 1a). We give short

TABLE 1. Key characteristics of the observatories.

Characteristic	Nama Karoo (northern)		Nama Karoo (central)		Succulent Karoo	
	Narais	Duruchaus	Gellap Ost	Nabaos	Remhoogte	Paulshoek
Vegetation unit	highland savanna		dwarf shrub savanna		Namaqualand blomveld	
Nearest town	Rehoboth		Keetmanshoop		Garies	
Location	23°12′ S, 16°89′ E		26°40′ S, 18°00′ E		30°38′ S, 18°27′ E	
Topography	slightly undulating		slightly undulating		rocky hills, sandy valleys	
Altitude (m above sea level)	1624		1099		1100	
Dominant soil group	calcisols		regosols		leptosols	
Annual rainfall (mm)	289		153		252	
Aridity index (UNEP)	0.20 (semiarid)		0.10 (arid)		0.12 (arid)	
Rainfall season	summer		summer		winter	
Mean annual temp. (°C)	18.6		21.0		15.3	
Contrasting management since	1980s		1980s		1950s	
Recommended stocking rate (ha/SSU)	2		10		12	
Recommended stocking rate (SSU/ha)	0.50		0.10		0.08	
Actual stocking rate (ha/SSU)	3.1	1.8	18	<8.7	>20	11.2
Actual stocking rate (SSU/ha)	0.32	0.56	0.06	>0.11	<0.05	0.09
Grazing intensity	lighter	heavier	lighter	heavier	lighter	heavier
Grazing regime	rotational	continuous	rotational	continuous	rotational	continuous
Dominant kind of livestock	cattle, goats	sheep	sheep, cattle	goats, donkeys	sheep, goats, cattle	sheep, goats
Land tenure	private	private	state	communal	private	communal
Number of analyzed plots	19	20	19	20	18	16

Notes: Climatic data are derived from WorldClim (Hijmans et al. 2005). Ecological data and stocking numbers are listed in Jürgens et al. (2010), except the stocking numbers in the Succulent Karoo, which were obtained from M. T. Hoffman (*personal communication*). Recommended stocking rates for a sustainable livestock production are listed in Limpricht and Naumann (2010) for the northern Nama Karoo, in Gibreel and Schneiderat (2010) for the central Nama Karoo, and in Todd and Hoffman (2009) for the Succulent Karoo. 1 SSU (small stock unit) = 1/6 LSU (large stock unit). Empty cells indicate that data for that observatory does not differ from the other observatory in the same biome.

descriptions of the study sites, while detailed information on the climate, soils, vegetation units, and livestock numbers of the six observatories can be found in Jürgens et al. (2010).

The first observatory pair (northern Nama Karoo) is located in central Namibia, about 25 km northwest of the town of Rehoboth. The area falls within the northern semiarid part of the Nama Karoo in the transition zone to the thornbush savanna. The vegetation belongs to the highland savanna unit (Giess 1971), and is characterized by grasses, scattered trees and shrubs, and a relatively high proportion of dwarf shrubs.

The second pair (central Nama Karoo) is located in southern Namibia, about 20 km north of the town of Keetmanshoop. It lies in the central, arid part of the Nama Karoo, and is characterized by open, grassy shrublands falling into the vegetation unit of dwarf shrub savanna (Giess 1971). The more heavily grazed observatory certainly represents the most severely impacted rangeland in our study.

The third pair (Succulent Karoo) is located in the north of South Africa, about 90 km southeast of the town of Springbok in the Kamiesberg Uplands. The site belongs to the Succulent Karoo biome, a winter-rainfall semidesert, which is recognized as a global biodiversity hotspot (Myers et al. 2000). Although classified as arid (aridity index 0.12) according to UNEP (UNEP 1992), its climatic characteristics of reliable annual rainfall, cool temperatures during the growing season, and high incidence of fog make conditions for plant growth similarly favorable to those in semiarid climates (Mucina et al. 2006). The vegetation falls into the unit of the Namaqualand blomveld, consisting of diverse communities of succulent dwarf shrubs (Mucina et al. 2006).

Data collection

A BIOTA biodiversity observatory encompasses an area of 1 km^2 that is subdivided into 100 1-ha plots, of which 20 were selected for vegetation monitoring, following a stratified-random procedure (Fig. 1b). Stratification was done according to physiognomically distinct habitat types to ensure that all types were represented adequately in the sample (for details, see

TABLE 2.   Overview of the diversity measures applied in the study.

Measure	Data type	Formula
Alpha diversity		
Evenness (Shannon; J)	cover	$H/\ln(S)$
Berger-Parker dominance ($D_{\text{B-P}}$)	cover	$C_{\max}/C_{\text{total}}$
Simpson diversity (D_{Simpson})	cover	$1 - \Sigma p_i^2$
Shannon diversity (H)	cover	$-\Sigma(p_i \times \ln[p_i])$
Richness (S)	incidence	number of entities
Beta diversity		
Bray-Curtis similarity	cover	$\sum|x_{ji} - x_{ki}|/\sum(x_{ji} - x_{ki})$
Jaccard similarity	incidence	$M/(M + N)$
z value†	incidence	$\log_{10}S1000 \text{ m}^2 - \log_{10}S100 \text{ m}^2$

Notes: S represents number of entities, $S1000 \text{ m}^2$ represents number of entities in a 1000-m^2 plot, $S100 \text{ m}^2$ represents number of entities in a 100-m^2 plot, C_{total} represents total vegetation cover in a plot, $C_{\max}$ represents cover of the most abundant entity, p_i represents proportional cover of entity i (i.e., cover of entity i/total cover), M represents number of entities with presence in both compared plots, N represents number of entities with presence in just one plot, and X_{ji}, X_{ki} represents cover of entity i in plots j and k, respectively. All were applied to species and functional groups (generic term: entities).

† Slope of species–area relationship in double-log space.

Jürgens et al. 2012). In the present study, those monitoring plots that were occupied by cropped fields or temporary river courses were excluded, so the number of analyzed plots per observatory varied between 16 and 20 (Table 1). Vegetation was sampled in the center of the hectare plots within two nested plots (Jürgens et al. 2012): an inner plot of 100 m^2 (10 × 10 m) and an outer plot of 1000 m^2 (20 × 50 m). The minimum distance between the fences and the plots was 80 m, except for two of the plots in the Succulent Karoo site, which were located close to the fence.

For each vascular plant species, the projected percent cover (Kent 2012) was estimated visually in the field. The sampling was conducted annually during the vegetation period in five consecutive years (2005–2009). As lowest cover value, we used 0.01% in the central Nama Karoo and Succulent Karoo, and 0.1% in the more densely vegetated northern Nama Karoo. For 100-m^2 plots, this would correspond to 0.01 m^2 or 0.1 m^2, respectively. Total cover of the vegetation was calculated from the summation of the cover values of all occurring species at the 100-m^2 scale. This is a sufficiently good approximation in drylands with sparse vegetation cover and limited overlap of individuals. For each monitoring plot, we additionally sampled a range of different abiotic parameters that were not directly influenced by grazing (inclination, surface cover of stones, and fractions of sand, silt, and clay in the uppermost soil horizon) to check for potentially confounding variables. Detailed descriptions of the sampling methods of the abiotic parameters can be found in Jürgens et al. (2010).

Statistical analyses

Statistical analyses were conducted separately for the three sites at a significance level of $\alpha = 0.05$. We tested for differences between the lighter and more heavily grazed observatories with permutation-based t tests

(Monte Carlo, 9999 permutations), because in many cases data were not normally distributed. For this, we used the R software package Exact RankTests (R Development Core Team 2008). First, we tested whether the abiotic parameters were sufficiently similar between plots on the lighter and more heavily grazed observatories. Plant diversity patterns were evaluated at the level of species and plant functional groups. For this purpose, all species were classified into 10 functional groups according to three different plant traits: life history (annual or perennial), growth form (forb, grass, geophyte, dwarf shrub [<0.5 m], shrub, or tree) and succulence (succulent or non-succulent). The resulting functional groups were annual forbs, annual grasses, perennial forbs, perennial grasses, geophytes, non-succulent dwarf shrubs, non-succulent shrubs, succulent dwarf shrubs, and succulent shrubs and trees.

The effect of grazing on vegetation cover was analyzed for both total cover and for cover per functional group based on interannual means. We then selected eight measures of alpha and beta diversity (Table 2) commonly applied in ecological studies (Magurran and McGill 2011). These measures included incidence-based as well as cover-based indices to account for both components of diversity: richness and evenness. All indices indicate higher diversity with increasing values, except for Berger-Parker dominance, Jaccard, and Bray-Curtis similarity, which decrease in value with increasing diversity.

All measures were applied at the 100-m^2 and 1000-m^2 scale (except for the z value that refers to the richness increase between the two scales), and on the species and functional group level. The diversity indices, as well as total vegetation cover, were first calculated separately for each of the five sampling years (2005–2009). We then averaged the values over the whole period in order to analyze the general impact during this time span (and not the year-specific responses biased by variable rainfall

TABLE 3.   Diversity measures by species and by functional group at heavier and lighter grazing intensities at a 100-m^2 scale.

Biome	Measure	Species			Functional groups		
		Lighter	Heavier	P	Lighter	Heavier	P
NNK	cover (%)	38.54 ± 4.56	28.76 ± 6.27	**<0.001**	38.54 ± 4.56	28.76 ± 6.27	**<0.001**
CNK	cover (%)	13.09 ± 5.26	8.64 ± 5.28	**0.012**	13.09 ± 5.26	8.64 ± 5.28	**0.012**
SK	cover (%)	19.19 ± 4.84	14.91 ± 5.51	**0.022**	19.19 ± 4.84	14.91 ± 5.51	**0.022**
NNK	evenness	0.61 ± 0.05	0.58 ± 0.13	0.314	0.66 ± 0.08	0.55 ± 0.17	**0.015**
CNK	evenness	0.66 ± 0.10	0.46 ± 0.11	**<0.001**	0.71 ± 0.12	0.48 ± 0.16	**<0.001**
SK	evenness	0.58 ± 0.09	0.53 ± 0.11	0.139	0.58 ± 0.09	0.47 ± 0.12	**<0.001**
NNK	Berger-Parker dominance	0.39 ± 0.08	0.43 ± 0.17	0.365	0.48 ± 0.10	0.60 ± 0.17	**0.011**
CNK	Berger-Parker dominance	0.39 ± 0.13	0.64 ± 0.15	**<0.001**	0.51 ± 0.11	0.73 ± 0.14	**<0.001**
SK	Berger-Parker dominance	0.34 ± 0.14	0.40 ± 0.17	0.263	0.49 ± 0.11	0.64 ± 0.15	**<0.001**
NNK	Simpson diversity	0.76 ± 0.06	0.72 ± 0.15	0.232	0.66 ± 0.09	0.54 ± 0.18	**0.011**
CNK	Simpson diversity	0.75 ± 0.11	0.52 ± 0.15	**<0.001**	0.63 ± 0.10	0.40 ± 0.16	**<0.001**
SK	Simpson diversity	0.79 ± 0.11	0.74 ± 0.14	0.259	0.62 ± 0.09	0.50 ± 0.14	**<0.001**
NNK	Shannon diversity	1.89 ± 0.21	1.84 ± 0.47	0.684	1.32 ± 0.17	1.08 ± 0.36	**0.012**
CNK	Shannon diversity	1.81 ± 0.33	1.09 ± 0.34	**<0.001**	1.21 ± 0.24	0.75 ± 0.29	**<0.001**
SK	Shannon diversity	2.02 ± 0.38	1.87 ± 0.44	0.321	1.18 ± 0.21	0.96 ± 0.24	**<0.001**
NNK	richness	23.26 ± 3.53	24.05 ± 4.37	0.550	7.42 ± 0.77	7.05 ± 0.83	0.172
CNK	richness	15.47 ± 2.84	12.10 ± 3.21	**<0.001**	5.68 ± 0.75	4.85 ± 0.99	**<0.001**
SK	richness	35.94 ± 8.26	34.44 ± 9.69	0.632	7.67 ± 0.59	8.00 ± 0.73	0.207
NNK	Bray-Curtis similarity	0.51 ± 0.10	0.41 ± 0.06	**<0.001**	0.68 ± 0.07	0.60 ± 0.07	**<0.001**
CNK	Bray-Curtis similarity	0.25 ± 0.08	0.15 ± 0.05	**<0.001**	0.46 ± 0.06	0.27 ± 0.04	**<0.001**
SK	Bray-Curtis similarity	0.25 ± 0.07	0.25 ± 0.09	0.914	0.62 ± 0.06	0.51 ± 0.12	**<0.001**
NNK	Jaccard similarity	0.45 ± 0.05	0.41 ± 0.05	**<0.001**	0.88 ± 0.04	0.84 ± 0.05	**0.011**
CNK	Jaccard similarity	0.26 ± 0.05	0.28 ± 0.06	0.198	0.81 ± 0.09	0.56 ± 0.07	**<0.001**
SK	Jaccard similarity	0.22 ± 0.04	0.22 ± 0.05	0.968	0.85 ± 0.06	0.85 ± 0.06	0.973
NNK	z value	0.20 ± 0.04	0.20 ± 0.09	0.967	0.05 ± 0.04	0.07 ± 0.05	0.222
CNK	z value	0.33 ± 0.08	0.35 ± 0.10	0.610	0.10 ± 0.06	0.17 ± 0.11	**0.025**
SK	z value	0.30 ± 0.08	0.27 ± 0.08	0.418	0.05 ± 0.03	0.03 ± 0.04	0.288

Notes: Data used for the index calculation were percent cover for the years 2005–2009; values are means ± SD. The diversity indices were calculated on the basis of species and plant functional groups. Significances were derived from permutation-based t tests run with the means of the indices over the five years; significant differences are shown in bold type ($P < 0.05$). NNK stands for northern Nama Karoo, CNK stands for central Nama Karoo, and SK stands for Succulent Karoo.

conditions). Further, we calculated the interannual standard deviations (SD) of the total vegetation cover and of each of the indices as a measure of the interannual variability.

The impact of grazing intensity on species composition at the 100-m^2 and 1000-m^2 scales was shown by nonmetric multidimensional scaling (NMDS), based on the mean cover values of the species for the period 2005–2009 (Bray-Curtis-similarity) using PAST (version 2.04, Hammer et al. 2001). In order to relate the changes in species composition to functional structure, we calculated the number of species within each functional group that belonged to one of the following response types: species that occur exclusively on the lightly grazed observatory (loss), species that occur exclusively on the more heavily grazed observatory (colonizer), species with lower cover in the more heavily grazed observatory (decreaser), and species with higher cover in the more heavily grazed observatory (increaser).

RESULTS

Diversity patterns in the different ecosystems

On the lighter-grazed observatories, the mean total plant cover ranged from nearly 40% in the northern Nama Karoo to only 19% in the Succulent Karoo and 13% in the central Nama Karoo (Table 3). The total number of species per observatory pair was highest at the site in the Succulent Karoo (381), followed by the northern Nama Karoo (207), and then the central Nama Karoo (163). All 10 distinguished functional groups were present in the central Nama Karoo observatory pair, but only nine in the northern Nama Karoo and the Succulent Karoo.

The values of the diversity indices indicate that alpha diversity on the level of species was highest in the Succulent Karoo, whereas on the level of functional groups, it was highest in the northern Nama Karoo. Evenness of species and functional groups, as well as beta diversity (measured as similarity and z value) peaked in the central Nama Karoo (Table 3).

Abiotic conditions

None of the analyzed topographic and soil variables differed significantly among the pairs of observatories in the central Nama Karoo and the Succulent Karoo (Table 4). By contrast, the plots in the more heavily grazed observatory in the northern Nama Karoo were significantly more inclined, stonier, and richer in silt but less rich in sand than those on the lighter-grazed observatory (Table 4). While being statistically significant, these differences were small compared to the differences between the sites, and typically smaller than the standard deviation within one of these observatories.

TABLE 4. Abiotic parameters at heavier and lighter grazing intensities in the uppermost soil horizon.

Biome	Measure	Lighter	Heavier	P
NNK	inclination (°)	0.16 ± 0.41	1.98 ± 3.42	**0.001**
CNK	inclination (°)	8.26 ± 11.46	4.80 ± 2.09	0.237
SK	inclination (°)	7.44 ± 5.37	10.31 ± 6.80	0.185
NNK	stone cover (%)	5.79 ± 4.16	11.10 ± 10.00	**0.029**
CNK	stone cover (%)	7.39 ± 8.98	4.70 ± 5.09	0.251
SK	stone cover (%)	22.25 ± 13.82	25.44 ± 1.82	0.652
NNK	sand (%)	75.50 ± 8.92	65.68 ± 7.88	**0.001**
CNK	sand (%)	48.77 ± 18.96	59.64 ± 17.66	0.105
SK	sand (%)	78.32 ± 7.54	81.90 ± 9.17	0.260
NNK	silt (%)	21.58 ± 8.13	29.87 ± 8.52	**0.009**
CNK	silt (%)	39.10 ± 20.35	30.19 ± 16.67	0.173
SK	silt (%)	17.35 ± 6.09	13.83 ± 6.74	0.152
NNK	clay (%)	3.50 ± 2.29	4.45 ± 1.14	0.081
CNK	clay (%)	12.13 ± 7.97	10.17 ± 7.73	0.524
SK	clay (%)	4.44 ± 2.38	4.60 ± 2.48	0.883

Notes: Values are mean ± SD. P values were derived from permutation-based t tests; bold type indicates significance. For biome definitions, see Table 3. For details of sampling methods, see Jürgens et al. (2010).

Grazing effects on species diversity

At the species level, the responses of alpha diversity to grazing intensity were significant almost only in the central Nama Karoo (Fig. 2, Table 3, and Appendix A). Here, the more heavily grazed observatory showed a significant decline at the 100-m^2 as well as at the 1000-m^2 scale in species richness, Shannon and Simpson diversity, evenness, and complementarily, a significant increase in Berger-Parker dominance. In the northern Nama Karoo and the Succulent Karoo, responses were not significant. The responses of the beta diversity measures were most consistent and pronounced in the northern Nama Karoo (Fig. 2), showing an increase in diversity at heavier grazing intensity, as indicated by a significantly decreased Bray-Curtis and Jaccard similarity (Table 3 and Appendix A). Likewise, beta diversity tended to increase in the more heavily grazed observatories in the other ecosystems, but the significance of results varied between indices and scales.
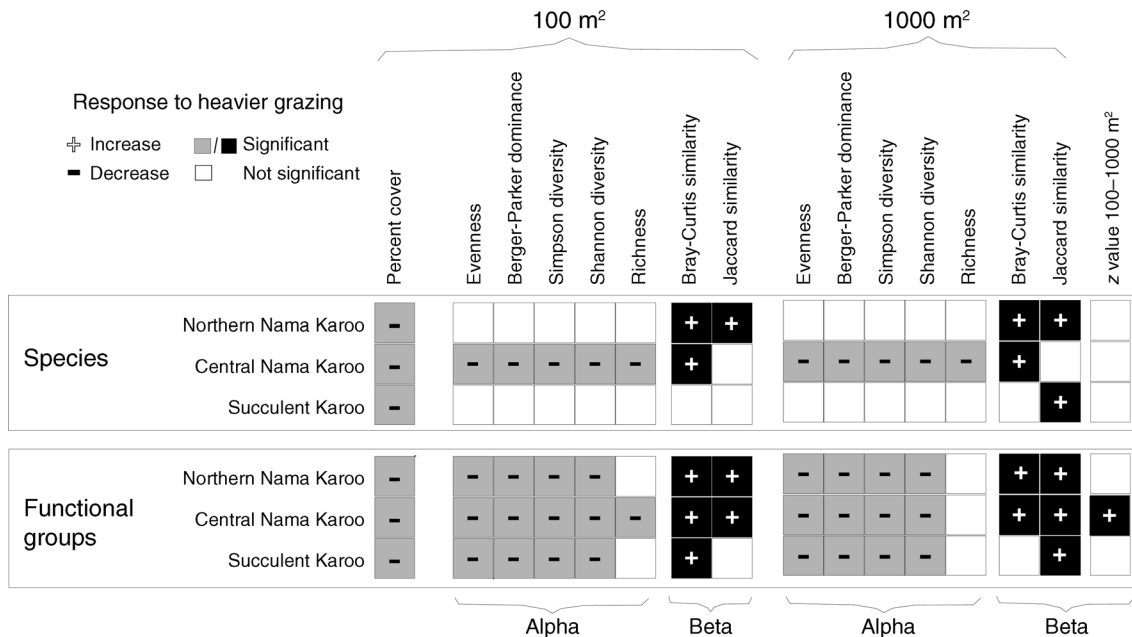

FIG. 2. Effects of heavier grazing on measures of alpha and beta diversity at two spatial scales (100 m^2 and 1000 m^2), evaluated at the level of species and of plant functional groups. The figure synthesizes the results given in Table 3 and Appendix A. Minus signs indicate a decrease and plus signs an increase in diversity. Note that the signs refer to diversity and not to the index values, i.e., decreases in Berger-Parker dominance and of the Jaccard and Bray-Curtis similarity indices are indicated as diversity increases, and vice versa. Significances were derived from permutation-based t tests ($P < 0.05$) run with average index values of five years (2005–2009). Significant results are indicated by shading, with lighter shading for significant decreases in diversity and darker shading for significant increases in diversity.
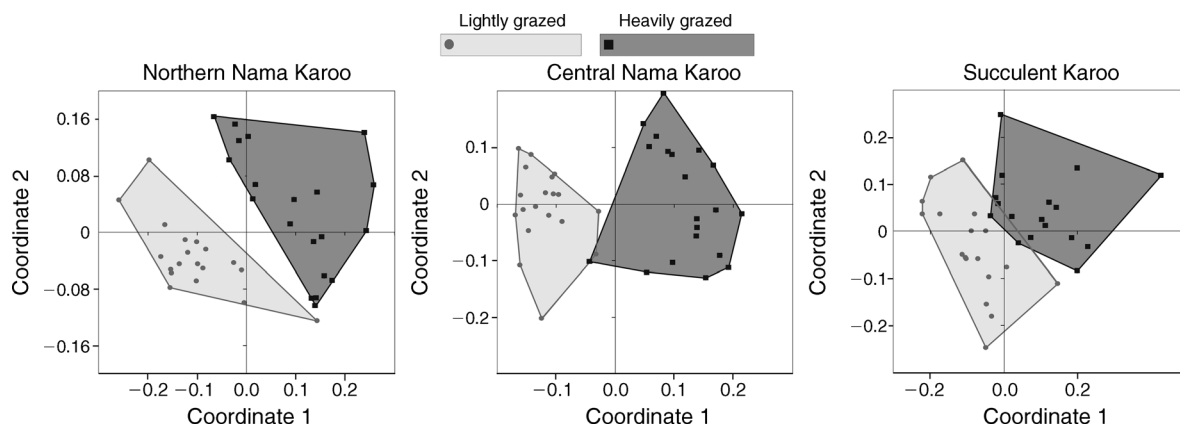
FIG. 3. Nonmetric multidimensional scaling (NMDS) ordination (Bray-Curtis) of the species compositions in the plots based on species mean cover values for the period 2005–2009 at a 100-m^2 scale. Stress values are 0.158 in the northern Nama Karoo, 0.259 in the central Nama Karoo, and 0.197 in the Succulent Karoo. Circles and lighter shading represent lightly grazed plots, squares and darker shading represent heavily grazed plots.

Grazing effects on diversity of plant functional groups

Contrary to the results of the species-level analysis, the response of the alpha diversity measures based on functional groups was highly consistent across ecosystems and scales (Fig. 2, Table 3, and Appendix A). In all three sites at both spatial scales, the cover-based indices, Shannon diversity, Simpson diversity, and evenness, significantly declined, and Berger-Parker dominance significantly increased at heavier grazing. A significant decrease of functional group richness was found only for the central Nama Karoo at the 100-m^2 scale.

Values of Bray-Curtis and Jaccard similarity indices significantly decreased at both scales in the more heavily grazed observatories in the central and northern Nama Karoo (Table 3, Appendix A), indicating an increase in beta diversity (Fig. 2). This shows that the heterogeneity of the functional composition was higher. In the Succulent Karoo, the significance of the increase in beta diversity on the more heavily grazed observatory varied among indices and spatial scales.

Grazing effects on species composition and functional structure

Total plant cover was significantly reduced in the more heavily grazed observatories. It decreased by about 25% in the northern Nama Karoo, about 30% in the central Nama Karoo, and about 22% in the Succulent Karoo (Table 3). The NMDS ordination shows at all sites a clear separation of the plots in the more heavily and lightly grazed observatories (Fig. 3, Appendix B), indicating that species composition and abundance patterns differed markedly across the fencelines.

At all sites, a similar proportion of species (40–50%) occurred exclusively on either side of the fence. The alteration of species composition by heavier grazing was due to declines in cover and total loss, as well as increases in cover and addition of new species (Table 5). In the northern Nama Karoo and Succulent Karoo, the proportions of lost or decreasing, and of increasing or colonizer species were balanced (about 50% each), whereas in the central Nama Karoo grazing-sensitive species (i.e., lost or decreasing species) dominated the overall species pool (67%).

The effects of heavier grazing on the cover of the functional groups varied between the studied sites (Fig. 4). In the northern Nama Karoo, the cover of annual grasses and succulent dwarf shrubs significantly declined. In the central Nama Karoo, a significant, nearly total loss of perennial grasses resulted in an open shrubland with an inter-shrub matrix dominated by annuals. Further, perennial forbs and non-succulent dwarf shrubs significantly decreased, whereas succulent shrubs significantly increased. In the Succulent Karoo, a significant decrease of succulent shrub cover and a significant increase of perennial forb cover occurred.

Grazing effects on interannual variability

The indices of alpha diversity showed in many cases significant increases in interannual variability under heavier grazing intensity in the central Nama Karoo and the Succulent Karoo at the level of species, and in all three ecosystems at the level of plant functional groups (Fig. 5, Table 6, and Appendix C). For example, the interannual variability of Simpson diversity at the level of plant functional groups significantly increased by about 40% in the northern Nama Karoo (from 0.05 to 0.07) and the central Nama Karoo (from 0.14 to 0.20), and was doubled in the Succulent Karoo (from 0.04 to 0.08) at the 100-m^2 scale.

In the central Nama Karoo and the Succulent Karoo, more significant increases occurred at the 100-m^2 compared to the 1000-m^2 scale, while for the northern Nama Karoo the opposite was true. The interannual

TABLE 5. Loss and colonization dynamics of plant species within functional groups.

Biome and plant functional group	Loss	Decreaser	Increaser	Colonizer	Total
Northern Nama Karoo					
Annual forb	17	16	5	6	44
Annual grass	3	5	3	0	11
Geophyte	1	2	2	6	11
Perennial forb	3	7	8	3	21
Perennial grass	4	6	5	2	17
Succulent dwarf shrub	2	1	0	2	5
Tree	0	1	0	0	1
Non-succulent dwarf shrub	2	4	9	7	22
Non-succulent shrub	0	1	2	2	5
Total	32	43	34	28	137
Central Nama Karoo					
Annual forb	7	13	5	6	31
Annual grass	4	5	2	1	12
Geophyte	3	0	0	1	4
Perennial forb	8	4	2	3	17
Perennial grass	1	5	1	0	7
Succulent dwarf shrub	0	0	0	2	2
Succulent shrub	0	0	0	1	1
Tree	0	2	0	0	2
Non-succulent dwarf shrub	6	5	5	1	17
Non-succulent shrub	6	7	4	3	20
Total	35	41	19	18	113
Succulent Karoo					
Annual forb	11	19	12	11	53
Annual grass	1	2	1	0	4
Geophyte	13	14	15	15	57
Perennial forb	3	3	12	9	27
Perennial grass	2	1	3	0	6
Succulent dwarf shrub	15	13	21	10	59
Succulent shrub	6	4	1	7	18
Non-succulent dwarf shrub	5	9	2	8	24
Non-succulent shrub	8	11	7	7	33
Total	64	76	74	67	281

Notes: The table shows four response types: species that exclusively occur in the more lightly grazed observatory (loss), species that occur exclusively in the more heavily grazed observatory (colonizer), species with lower cover in the more heavily grazed observatory (decreaser), and species with higher cover in the more heavily grazed observatory (increaser). Assignments are based on mean cover values for the years 2005–2009 at the 100-m^2 scale.

variability of the beta diversity indices and of the total plant cover responded inconsistently to heavier grazing across ecosystems and scales.

DISCUSSION

Drawing conclusions from the fence-line contrasts

Fence-line contrasts are widely utilized to analyze long-term effects of contrasting land-tenure systems and grazing intensities on spatiotemporal patterns in vegetation (e.g., Todd and Hoffman 2009, Rutherford and Powrie 2010, Dreber et al. 2011). One could argue that fence-line contrasts such as those in our study suffer from pseudoreplication (Hurlbert 2004), because in each ecosystem we had only one more heavily and one more lightly grazed observatory. Therefore, theoretically the differences found could have been caused by another environmental factor than grazing intensity that differed in parallel. Fence-line contrasts are natural experiments (Todd and Hoffman 2009), and due to environmental heterogeneity at landscape scale, they cannot realistically be replicated (Rutherford and Powrie 2010). In such a situation, the only way to attribute detected differences to grazing regime is to check for differences in other factors that, according to ecological knowledge, could influence plant diversity (see Quinn and Keough 2002, p. 160). As the pairs of observatories were a priori selected with the aim of high similarity in all other factors than grazing, and because our analyses of topographic and soil variables yielded no significant differences for two pairs and significant differences of a small effect size in the last pair of observatories, we argue that the differences found in plant diversity are indeed attributable to differences in grazing.

While the grazing regime differences between each of the neighboring observatories had existed for a couple of decades, they concern more than one factor (Table 1). Most importantly, both stocking rate (ha/small stock unit) and grazing system (continuous vs. rotational) always varied simultaneously. Increased grazing and/or browsing pressure was always interrelated with continuous stocking above the locally recommended rates, whereas lower grazing pressure was consistently char-

acterized by rotational stocking below the recommended stocking rate (Table 1). A separate examination of these land-use components was therefore not feasible, nor would it have been ecologically meaningful, as the connection of the two factors is typical for the rangelands of the region. Therefore, as in other ecological studies aiming at a general synthesis, different factors have been combined into a single variable, like grazing intensity (Todd and Hoffman 2009, Rutherford et al. 2012). Similarly, in our study it was not possible to integrate and account for differences in the predominating type of livestock (i.e., grazer vs. browser) across the fence-lines. It should be noted, however, that these systems can be regarded as in a stable state of lower productivity, where grazers are forced to browse available shrub phytomass, particularly in the dry season, and browsers also graze the herbaceous vegetation component in the wet season. On the contrary, in all ecosystems studied, palatable dwarf shrubs are a characteristic floristic element of the lightly grazed vegetation (Jürgens et al. 2010), which are also well-utilized by grazers throughout the year. Thus, potentially differential effects of different livestock types on plant diversity patterns are assumed to be of lower importance than the grazing intensity analyzed. This assumption is in agreement with the diversity trends showing more or less the same direction in all three fence-line contrasts, despite variations of livestock types.

Alpha diversity of species

Consistently across ecosystems, the total plant cover was reduced and the species composition markedly altered on the more heavily grazed observatories. However, a significant decrease in species alpha diversity was detected only in the central Nama Karoo. The lack of significant responses in species diversity at the other sites is in line with a number of field studies in southern African drylands, which found that grazing-induced changes in vegetation structure may have little effect on species richness (e.g., Todd and Hoffman 2009). In a series of fence-line studies, Rutherford and Powrie (2010) and Rutherford et al. (2012) even found positive effects of heavier grazing on Shannon diversity and evenness. Together, the results suggest that the assumed negative effect of livestock grazing on alpha diversity of plant species in the Succulent Karoo and Nama Karoo (e.g., Milton et al. 1994, Mucina et al. 2006) is not general (see also Rutherford et al. 2012).

In their recent modification of the model of grazing effects by Milchunas et al. (1988), Cingolani et al. (2005) suggest that in systems with a long grazing history, the selective pressure of herbivores has fluctuated over time, allowing the development of different pools of species adapted to low or high grazing intensities. The grazing-resistant pool increases in periods of high grazing intensity, and the less grazing-resistant pool increases in periods of lower grazing intensity. When the number of species in these divergent pools is similar, changes in
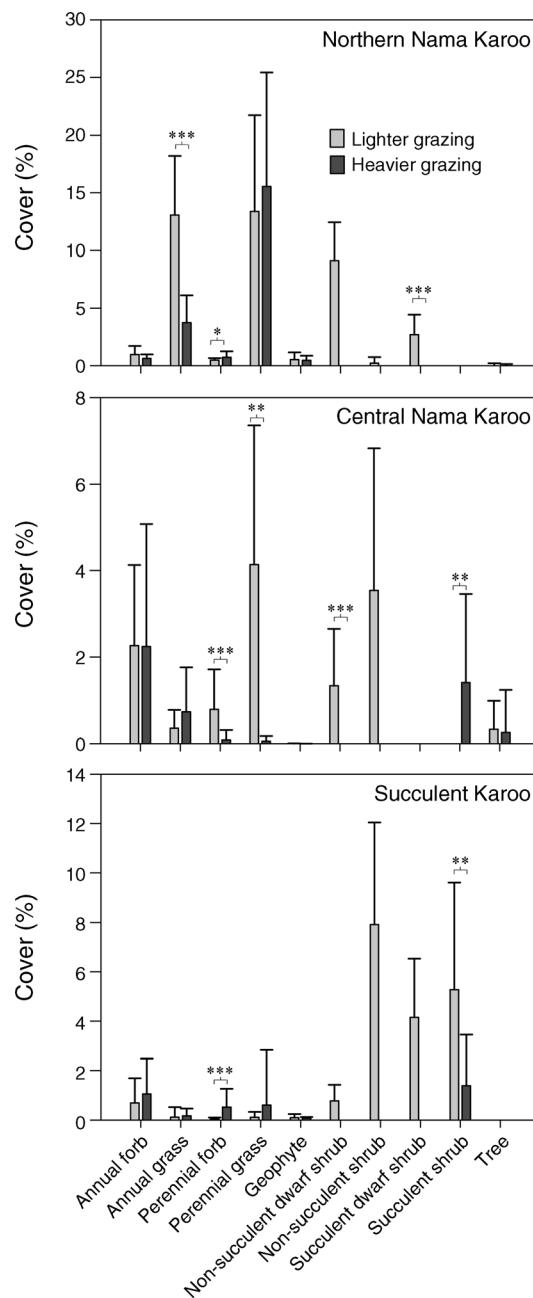

FIG. 4. Percent cover of the functional groups at heavier and lighter grazing intensities. Data are means with SD for the years 2005–2009 at the 100-m² scale. Significances were derived from permutation-based t tests run with the cover means over the five years; asterisks indicate significant differences.
* P < 0.05; ** P < 0.01; *** P < 0.001.

grazing intensity can cause substantial changes in composition with little or no change in species diversity. Our study region falls into this category of systems with low productivity and a long evolutionary history of grazing (Smith 1999) and, at least in case of the northern Nama Karoo and Succulent Karoo sites, corresponds well to this aspect of the model. Our results for these
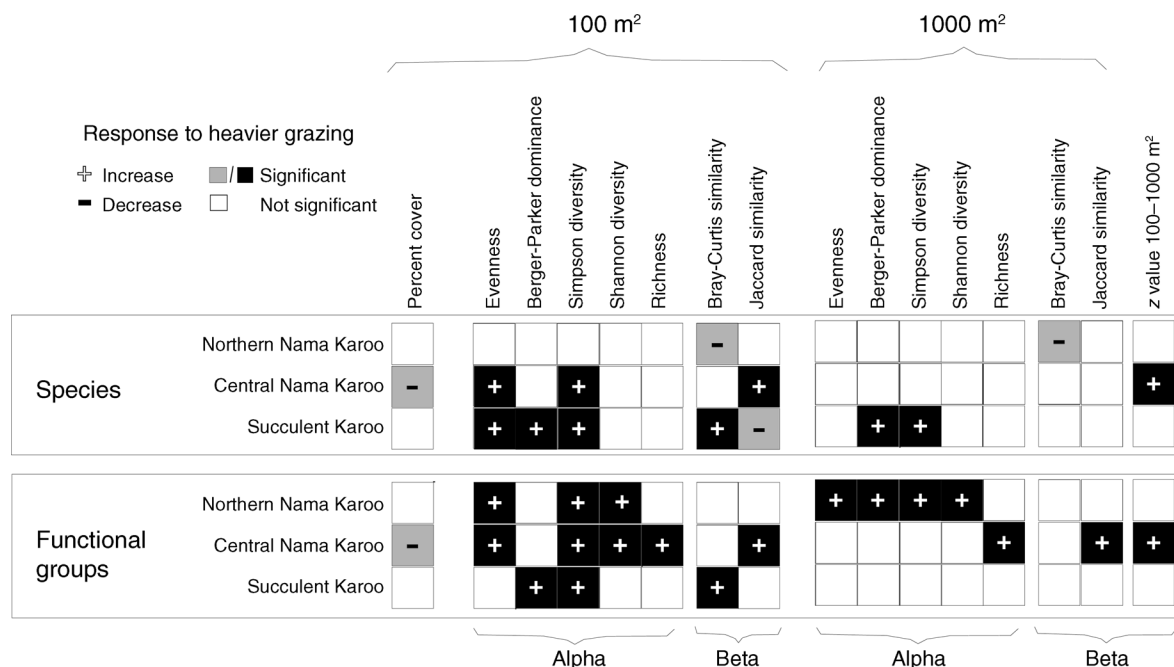
Fig. 5. Effects of heavier grazing on the interannual variability expressed as SD of total plant cover and the diversity indices at two spatial scales, evaluated at the level of species and of plant functional groups. Minus signs indicate a decrease and plus signs an increase in SD. Significances were derived from permutation-based t tests ($P < 0.05$) run with the SDs of five years (2005–2009). Significant results are indicated by shading, with lighter shading for significant decreases in SD and darker shading for significant increases in SD.

Table 6. Interannual standard deviations of total plant cover and the diversity indices by species and by functional group at heavier and lighter grazing intensities at a 100-m² scale.

Biome	Measure	Species			Functional groups		
		Lighter	Heavier	P	Lighter	Heavier	P
NNK	cover (%)	9.10 ± 2.75	8.32 ± 2.55	0.339	9.10 ± 2.75	8.32 ± 2.55	0.339
CNK	cover (%)	6.85 ± 2.35	4.67 ± 4.37	**0.028**	6.85 ± 2.35	4.65 ± 3.35	**0.027**
SK	cover (%)	2.23 ± 1.15	3.79 ± 3.93	0.112	2.23 ± 1.15	3.79 ± 3.93	0.112
NNK	evenness	0.05 ± 0.02	0.06 ± 0.03	0.735	0.06 ± 0.02	0.07 ± 0.02	**0.029**
CNK	evenness	0.12 ± 0.07	0.19 ± 0.08	**0.010**	0.15 ± 0.07	0.22 ± 0.07	**0.002**
SK	evenness	0.03 ± 0.01	0.06 ± 0.05	0.007	0.05 ± 0.02	0.07 ± 0.04	0.055
NNK	Berger-Parker dominance	0.09 ± 0.03	0.09 ± 0.04	0.710	0.08 ± 0.03	0.09 ± 0.03	0.796
CNK	Berger-Parker dominance	0.14 ± 0.07	0.19 ± 0.08	0.054	0.14 ± 0.05	0.16 ± 0.06	0.257
SK	Berger-Parker dominance	0.04 ± 0.02	0.09 ± 0.08	**0.014**	0.04 ± 0.03	0.08 ± 0.05	**0.021**
NNK	Simpson diversity	0.06 ± 0.02	0.06 ± 0.04	0.753	0.05 ± 0.02	0.07 ± 0.02	**0.009**
CNK	Simpson diversity	0.14 ± 0.09	0.22 ± 0.08	**0.004**	0.14 ± 0.06	0.20 ± 0.07	**0.006**
SK	Simpson diversity	0.03 ± 0.02	0.07 ± 0.07	**0.019**	0.04 ± 0.02	0.08 ± 0.05	**0.005**
NNK	Shannon diversity	0.21 ± 0.08	0.23 ± 0.11	0.486	0.11 ± 0.04	0.15 ± 0.04	**0.011**
CNK	Shannon diversity	0.47 ± 0.14	0.54 ± 0.18	0.195	0.30 ± 0.09	0.38 ± 0.10	**0.022**
SK	Shannon diversity	0.14 ± 0.07	0.20 ± 0.15	0.168	0.10 ± 0.05	0.14 ± 0.09	0.153
NNK	richness	5.05 ± 1.62	5.53 ± 1.56	0.356	0.26 ± 0.26	0.26 ± 0.32	0.935
CNK	richness	5.62 ± 1.84	5.89 ± 1.55	0.644	1.07 ± 0.48	1.79 ± 0.40	**<0.001**
SK	richness	7.75 ± 2.56	6.10 ± 2.11	0.054	0.64 ± 0.37	0.64 ± 0.21	0.980
NNK	Bray-Curtis similarity	0.06 ± 0.02	0.04 ± 0.02	**0.039**	0.04 ± 0.02	0.04 ± 0.02	0.724
CNK	Bray-Curtis similarity	0.05 ± 0.02	0.05 ± 0.02	0.469	0.09 ± 0.04	0.07 ± 0.03	0.084
SK	Bray-Curtis similarity	0.01 ± 0.01	0.03 ± 0.02	**<0.001**	0.03 ± 0.01	0.06 ± 0.03	**<0.001**
NNK	Jaccard similarity	0.03 ± 0.01	0.02 ± 0.01	0.078	0.03 ± 0.02	0.04 ± 0.03	0.551
CNK	Jaccard similarity	0.06 ± 0.02	0.10 ± 0.02	**<0.001**	0.15 ± 0.04	0.18 ± 0.03	**0.012**
SK	Jaccard similarity	0.03 ± 0.01	0.02 ± 0.01	**<0.001**	0.05 ± 0.03	0.04 ± 0.02	0.139
NNK	z value	0.05 ± 0.02	0.04 ± 0.02	0.229	0.02 ± 0.02	0.02 ± 0.02	0.420
CNK	z value	0.10 ± 0.06	0.16 ± 0.07	0.003	0.09 ± 0.06	0.15 ± 0.06	**0.003**
SK	z value	0.05 ± 0.03	0.05 ± 0.02	0.283	0.03 ± 0.02	0.03 ± 0.01	0.346

Notes: Data used for the index calculation were percent cover for the years 2005–2009; values are means ± SD. The diversity indices were calculated on the basis of species and plant functional groups. Significances were derived from permutation-based t tests run with the SDs of the indices over the five years ($P < 0.05$). For biome definitions, see Table 3. Bold face type indicates significant P value.

sites suggest that following the model by Cingolaini et al. (2005), losses and decline of grazing-sensitive species may have been compensated for by increases and colonization of grazing-tolerant species (Table 5).

The significantly lower alpha diversity in the more heavily grazed central Nama Karoo site calls for an explanation. Compared to the other sites, this particular observatory is the most impacted by intense livestock grazing. The number of colonizer species could not compensate for the species lost in response to heavier grazing (see Table 5). Severe grazing may increase the probability of local extinction of species (O'Connor 1991, Todd 2006), and changes in the competitive environment can lead to an overall dominance of a few species and the development of rather species-poor, grazing-adapted plant communities (Bestelmeyer et al. 2003, Dreber et al. 2011). Despite the generally high resilience of the Nama Karoo vegetation to grazing pressure (Todd 2006), grazing regimes that are beyond the historical range experienced by the system can induce a decline in species diversity (Cingolani et al. 2005).

Alpha diversity of plant functional groups

In contrast to the result for species diversity, alpha diversity of plant functional groups decreased at heavier grazing very consistently across ecosystems and scales. However, functional group richness responded less sensitively and less consistently than the cover-based measures. The reason for this is that most functional groups were reduced but remained present, i.e., richness was not affected, whereas cover-based indices, which respond to changes in cover and dominance patterns (cf. Mouillot et al. 2013), showed significant effects.

The decreases in functional group evenness show that the dynamics of species loss, decrease, increase, and colonization were not evenly distributed across functional groups. According to a recent synthesis by Mouillot et al. (2013), continuous disturbance leads to a clustered occurrence of species with certain functional traits. Vulnerable species decline, while newly occurring species are functionally redundant with those already present. Increased functional redundancy within grazing-tolerant response types causes an increase in functional dominance, and conversely, a decline in functional evenness (Díaz and Cabido 2001). This mechanism can be clearly observed in our sites. For example, the reduction of succulent shrubs was accompanied by the dominance of non-succulent shrubs in the more heavily grazed observatory in the Succulent Karoo. In the central Nama Karoo, a disproportionate loss of large and competitive perennial grasses changed the vegetation towards an open shrubland with an inter-shrub matrix dominated by annuals. A previous study by Dreber et al. (2011) conducted at the same site revealed a large differential effect of the disturbance regime on the abundance patterns of functional groups. According to that study, heavier grazing favored species

with specific traits, permitting them to persist under the severe impacts of small stock, which in the long term resulted in a local species pool dominated by small-seeded prostrate forbs and annual, largely unpalatable grasses.

In the dryland biomes of southern Africa, quantification of disturbance effects on functional diversity has been lacking until now. In contrast, in Mediterranean winter-rainfall ecosystems, functional diversity has been increasingly used to describe diversity patterns in rangelands. Functional diversity (measured as Rao's diversity coefficient) and species diversity (Simpson diversity) have been shown to follow divergent responses to grazing in Mediterranean systems (de Bello et al. 2006, Carmona et al. 2012), mirroring the results of our current study. However, the response direction differed in these two Mediterranean studies. Along a rainfall gradient (325–925 mm/yr), de Bello et al. (2006) found negative effects of grazing on functional diversity only under more humid conditions. There were no effects on functional diversity at the arid end of the gradient (which still received more rainfall than any of our study sites). On the other hand, Carmona et al. (2012), who studied a Mediterranean ecosystem with 540-mm mean annual rainfall, found negative effects of grazing on functional diversity, particularly for drier, water-limited habitats. These dry habitats might be more comparable to the conditions in our study area.

Along the aridity gradient of our study, effects on functional diversity increased with increasing aridity, as expressed by lower P values and an increasing difference in the mean index values between the neighboring observatories. This pattern might have been enhanced by the coincidence of the most severe excess of the recommended stocking rate and the most arid conditions. However, we suggest that the stronger response at drier conditions is also related to the fact that functional redundancy (i.e., number of species within a functional group sensu Walker 1992) tends to be lower in dry, compared to more humid rangeland systems (de Bello et al. 2009). Likewise in our study, the most arid site (central Nama Karoo) had the lowest number of species per functional type (cf. Table 5). If the redundancy within a functional group is lower, land use is more likely to induce a loss (or notable decrease) of this group (Díaz and Cabido 2001, Cadotte 2011).

In this study, we defined functional diversity simply as the number of a priori defined functional groups (sensu Lavorel et al. 1997) based on growth forms. This aggregation of functional information may lead to a loss of information (Fonseca and Ganade 2001, Petchey and Gaston 2006), or to a low explanatory power of ecosystem processes (Wright et al. 2006). In our case, contrasting trends of the same functional group at the different sites may have occurred because of functional divergence within this group. Nevertheless, comparisons across large geographical ranges, as in our investigation, may be more appropriate with the use of a reduced set of

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a priori defined groups, since appropriate trait sampling is often not feasible, and overlap of trait values between sites becomes more unlikely.

Beta diversity

The impact of grazing intensity on beta diversity was less consistent across ecosystems and scales than the impact on alpha diversity. There was also no clear pattern in the response of species vs. functional diversity, or of cover-based vs. richness-based indices. However, the overall trend was one of beta diversity being higher in the more heavily grazed observatories, i.e., the heterogeneity of the community composition and the functional structure between plots increased with heavier grazing.

Although we found no difference in the effects of grazing on diversity between the 100-m^2 and 1000-m^2 scale, the opposite effects on alpha and beta diversity indicate that the spatial scale has a strong influence. It is likely that our study did not cover a sufficient range of grain sizes to be able to capture differences in species turnover. However, the increased beta diversity in our study confirms the results of other studies in semiarid and arid rangelands using a wider range of scales, which found that in some systems, the negative impact of grazing on species diversity ceased with increasing grain size (de Bello et al. 2007, Rutherford and Powrie 2010).

The increase of beta diversity with grazing is in line with the findings of Asner et al. (2004), who identified increased spatial heterogeneity of vegetation as an overarching pattern in desertification processes across ecosystems. The observed reduction of plant cover (and thus increased proportion of bare soil) in the more heavily grazed observatories might lead to elevated beta diversity by raising the degree of vegetation patchiness and heterogeneity of resource distribution (Hendricks et al. 2005, de Bello et al. 2007). Spatial heterogeneity can also arise from localized urine and dung deposition, trampling paths, and erosion rills (Olff and Ritchie 1998). Microsites then filter for a variety of adapted colonizer species (Landsberg et al. 2002, Dreber and Esler 2011). Such phenomena are well exemplified by grazing systems, in which the temporal and spatial availability of key resources (water often being the most important) creates gradients of grazing intensity and resultant productivity. At high stocking rates, the areas around water points are exposed to extreme conditions of grazing and trampling, creating a "sacrifice zone" (Andrew 1988; Wesuls et al. 2013), whereas the more remote, or less accessible, rocky areas may be little affected by grazing (Anderson and Hoffman 2007). In the more heavily grazed observatories, the higher disturbance impacts by livestock near water points and the more pronounced grazing gradient over longer distances resulted in a high amount of small-scale environmental patchiness. In comparison, the lightly grazed observatories exhibit rather short grazing-intensity gradients, and thus lower beta diversity.

Interannual variability

Our repeated sampling over five years gave us the opportunity to relate interannual variability of vegetation cover and various aspects of plant diversity to grazing intensity. As variability can be seen as the reciprocal value of stability, this is an important aspect, from the perspective of land users, who are interested in little variation of biomass production over the years (Snyman 1998). Nevertheless, according to a search in the *Web of Science* (search terms "grazing intensity" AND "diversity variability" OR "interannual"; 7 July 2013), this has hardly ever been studied before. One of the few studies that addressed the effect of grazing intensity on the stability of rangeland diversity is Sternberg et al. (2000), whose Fig. 3 suggests a higher interannual variability of species richness under higher grazing intensity, although the authors did not test this statistically. In our study, we found mostly increased variability, i.e., decreased stability, of plant alpha diversity under heavier grazing. This effect was not always significant, stronger for functional diversity than for species diversity, and stronger at the 100-m^2 scale than at the 1000-m^2. Our study thus seems to be among the first to demonstrate that grazing intensity not only affects mean diversity, but also negatively affects the stability of diversity, which has important implications for biodiversity conservation in the context of climate change. As the interannual variability of species richness in arid rangelands is mainly driven by precipitation variability, these fluctuations would further increase with the higher rainfall variability projected for the future (Haensler et al. 2010), and be exacerbated by overly intense grazing. Regarding stability of vegetation cover (which can be seen as a proxy of biomass production) and beta diversity, our findings are inconsistent across sites, and call for further studies in a wider array of ecosystems.

Conclusions

The patterns of plant diversity found in this study may contribute to a more general understanding of land-use effects across arid and semiarid ecosystems, as well as to better-founded approaches in environmental conservation and management.

Firstly, the choice of metric used to quantify diversity is important. The diverging response of species richness and abundance-based diversity indices is the subject of an ongoing debate in disturbance ecology (reviews by Mackey and Currie 2001, Svensson et al. 2012). Specifically, it has been recognized that species richness is of limited indicative value if applied alone, because it needs extinction to be reactive (Purvis and Hector 2000). Our results confirm that the same argument applies to measures of functional diversity. A community can be considered more diverse if distinct functional groups are equally abundant than if one or few groups dominate (Petchey and Gaston 2006, Mouillot et al. 2013). Therefore, at the functional level as at the species level,

the concept of diversity should not be used without reference to its richness and evenness components.

Secondly, changes related to rangeland degradation could be better detected and described at the level of functional groups than at the level of species. The finding of a clearer and more consistent response of functional diversity compared to species diversity seems to be a pattern that is broadly applicable. Stronger responses of functional diversity have been demonstrated in previous studies for different disturbances types, taxa, and ecosystems. Examples are ground beetle communities after flood disturbance in river meadows (Mouillot et al. 2013), amphibian communities after logging in tropical forests (Ernst et al. 2006), and fish communities in the Gulf of Mexico (Villéger et al. 2010). This shows that functional diversity is a highly important aspect in the understanding and quantification of the complex changes in disturbed ecosystems. Functional diversity also plays an important role in the conservation and management of ecosystems, because it is closely linked to ecosystem functioning (de Bello et al. 2010, Cadotte 2011). The loss (or strong decline) of an entire functional type would have a larger impact on ecosystem functioning than the loss of the same number of species drawn from a variety of functional types (Díaz and Cabido 2001, Reiss et al. 2009). For example, in the central Nama Karoo, the loss of perennial grasses is coupled with a loss in perennial grazing resources for livestock, an increased vulnerability to soil erosion, and alteration of ecohydrological feedback mechanisms (Domptail et al. 2010). The change in ecosystem functioning may shift the systems across critical thresholds between alternative states of plant communities (López et al. 2011).

Finally, in cases where alpha diversity decreased under heavier grazing, beta diversity simultaneously increased, suggesting that in these situations, a decline in alpha diversity may, on the landscape scale, be mitigated by increased heterogeneity of the vegetation.

Altogether, our results reflect key structural changes in response to increased land-use intensity in the dryland biomes of southern Africa. Responses were stronger for functional group-based diversity indices than for species-based diversity indices. Indices of plant functional diversity that include evenness are a particularly sensitive tool to detect and quantify disturbance effects on ecosystems, and may be particularly helpful if the compared sites are situated along bioclimatic gradients, as between the drylands of South Africa and Namibia that have different species pools. However, the decision of which metric on which level should be chosen is ultimately determined by the purpose of a study. While it may be more suitable to apply a functional approach when, for example, determining indicators for ecosystem services, a taxonomic approach is needed for many conservation issues, be it compiling simple species lists or assessing species abundance patterns. In general, our results suggest that it is advisable for any study to include a set of complementary biodiversity metrics instead of a single one to achieve a comprehensive assessment and allow for sound comparisons with other studies.

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SUPPLEMENTAL MATERIAL

Appendix A

Diversity measures at heavier and lighter grazing intensities at a 1000-m^2 scale (*Ecological Archives* A024-069-A1).

Appendix B

Nonmetric multidimensional scaling ordination (Bray-Curtis) of species based on their mean cover values for the period 2005–2009 at a 1000-m^2 scale (*Ecological Archives* A024-069-A2).

Appendix C

Interannual standard deviations of total plant cover and the diversity measures at heavier and lighter grazing intensities at a 1000-m^2 scale (*Ecological Archives* A024-069-A3).