



Impacts of heavy grazing on plant species richness: A comparison across rangeland biomes of South Africa



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ABSTRACT

The net effect of heavy grazing and land degradation on plant diversity and richness is insufficiently understood for incorporation in national biodiversity assessments. A study was undertaken to determine the effects of heavy grazing primarily on richness of vascular plant species across the arid and semi-arid rangeland biomes of South Africa. Major grazing contrasts were systematically identified for sampling in rangelands of Succulent Karoo, Nama-Karoo, Thicket, Grassland, Kalahari dune savanna and Mopane savanna. The related parameters of species diversity, evenness and turnover were also examined and analysed at the whole site level. The study represents a new site-level comparison of earlier individual studies that also necessitated recalculation and standardization of original data, where appropriate. Impacts of heavy grazing on plant species richness were found to vary from negligible or slightly positive to distinctly negative, depending on site. The sharp reductions in richness may have been associated with special secondary conditions that can occur in arid areas. Species diversity did not track species richness well and was often dominated by species evenness patterns. Moderate to substantial turnover of species occurred, even with negligible change in species richness. Species turnover was largely associated with replacement of species, except on one site where turnover was more evenly split between its replacement and nestedness components. Heavy grazing altered species composition on all study sites, usually with reduced grazing quality and favouring annual plants. Surprisingly few of the replacement species on most of the study areas were alien or exotic. Remarkably, the magnitude of change in species richness across the limited rainfall gradient of the study often greatly exceeded changes associated with the heavy grazing levels at each site. Use of the significant non-linear relationship found between loss of plant canopy cover through grazing and the relative decline in species richness needs further exploration.

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1. Introduction

Land degradation, including overgrazing, is regarded as one of the main environmental problems in southern Africa (Darkoh, 2009). It has been suggested as the main cause of biodiversity loss in the arid shrublands and savannas of the region (Scholes and Biggs, 2005). In particular, excessively heavy grazing has been indicated to contribute to decline in biodiversity (Biggs et al., 2008). Indeed, there is a widely held assumption globally that livestock grazing reduces biodiversity in contrast to that expected in 'pristine or primary vegetation' (Alkemade et al., 2009). Furthermore, in the special case of South Africa, the legacy of land partitioned into often lightly stocked commercial and usually heavily stocked communal use has led to

communal land tenure being indicated nationally as the strongest predictor of vegetation and soil degradation (Hoffman and Ashwell, 2001; Vetter et al., 2006). However, the apparently deleterious effects of degradation through heavy grazing by domestic livestock on land under communal use are contentious (Shackleton, 1993; Ward et al., 1998; Sullivan and Rohde, 2002; Vetter and Bond, 2012).

The first South African National Spatial Biodiversity Assessment of 2004 was unable to incorporate the potentially important threats and impacts of habitat degradation on biodiversity. This omission was ascribed to an inadequate understanding of the relationship between land degradation and biodiversity loss in South Africa (Rouget et al., 2004). This problem prompted the South African National Biodiversity Institute to initiate a pilot research programme to suggest a way forward to assess the importance of the effects of degradation on plant diversity across the rangeland biomes of South Africa. The focus was on the effects of heavy grazing in the widespread semi-arid and arid parts of South Africa and included some areas under communal tenure. This pilot programme resulted in six recently published biome studies (Rutherford and Powrie, 2010a,b, 2011;

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Rutherford et al., 2012a,b,c) which took place partly in parallel and resulted in limited cross referencing and in few comparisons across the biome study areas. The current paper provides an opportunity for a fresh analysis of results across biomes that followed a broadly similar approach. Despite the similar sampling procedure across study sites it should be realised that some of these exploratory studies were necessarily tailored to local conditions with resultant differences in sample sizes. This paper is consequently limited to those species diversity and richness parameters which could be recalculated from original data and standardized where possible to allow valid cross comparisons across biome sites. In the process, a few minor corrections could be made. This paper also concentrates on pooled or combined species data per site which have not been reported consistently for these sites before.

Diversity and richness are sometimes used interchangeably without definition, which is unfortunate (see Rutherford et al., 2012a). Species richness is a simple count of species per specified size area whereas species diversity is more complex and depends on both species richness and the evenness of spread of abundance of each species (see further detail in Methods below).

Claims of decline in total plant diversity or species richness with heavy grazing or land degradation in the region are not consistently supported, yet it should be noted that studies with the necessary comprehensive species assessments are unfortunately relatively uncommon (O'Connor et al., 2010). Studies in which species richness clearly declined with grazing include those in thicket vegetation (Hoffman and Cowling, 1991; Lechmere-Oertel et al., 2005). Similarly, in grasslands of the Eastern Cape, a substantial decline in species richness was reported for heavily stocked communal areas compared to that in more lightly stocked commercial areas (Hoare, 2003). However, this contrasts with findings in mesic grassland areas that showed no significant effect of heavy grazing on plant species richness (Walters et al., 2006; Martindale, 2007). Results elsewhere range from a decline in species richness close to watering points or stock posts in Succulent Karoo (Beukes and Ellis, 2003; Hendricks et al., 2005) and Nama-Karoo (Todd, 2006), to no significant difference with grazing in Succulent Karoo (Todd and Hoffman, 1999; Petersen et al., 2004; Allsopp et al., 2007; Anderson and Hoffman, 2007; Haarmeyer et al., 2010 in part), to a significant increase in species richness in lowveld savanna (Shackleton, 2000).

In keeping with the variable regional results above on the impacts of grazing on species richness, a global analysis of specific studies has suggested that impacts of grazing of livestock on biodiversity can be negative and sometimes positive (Reid et al., 2010). Well known, but developing, theory in this regard takes the form of the generalized dynamic equilibrium model or grazing reversal hypothesis (Milchunas et al., 1988; May et al., 2009; Oesterheld and Semmartin, 2011) that predicts the effect of grazing intensity on plant species diversity depending on habitat resource level (aridity, also inversely reflected in productivity) and length of the evolutionary history of grazing for a given type of vegetation. This model is, in part, analogous or related to the earlier Huston dynamic equilibrium model and the intermediate-disturbance hypothesis (Milchunas et al., 1988). The site-scale model may be summarized as follows. For semi-arid, low productivity areas with long evolutionary history of grazing, the model expects a flat or slightly diminishing response of species diversity with grazing intensity, based on the assumption that selection from drought (aridity) and grazing resistance are convergent, and compositional changes in response to grazing are minimal (Cingolani et al., 2005). In semi-arid, low productivity areas with a short evolutionary history of grazing a steeper decline in diversity with grazing is expected since plants that evolved under low grazing intensity recover poorly from grazing, and, as with the other semi-arid category above, grazing is not expected to produce a release from competitive dominance that might substantially increase diversity. In sub-humid areas with high productivity and

long history of grazing the relationship between grazing intensity and species diversity takes the form of a hump-shaped curve (Cingolani et al., 2005). For sub-humid areas with high productivity but short evolutionary history of grazing, the release from dominance should cause species diversity to peak at a rather low grazing intensity (Milchunas et al., 1988; Cingolani et al., 2005). This model still needs to be tested over the range of environments in South Africa. The model appears to sanction species richness as a measure of species diversity (Cingolani et al., 2005; see Rutherford et al., 2012a).

Given the above perceptions and uncertainties, the main research question addressed was: Does species richness decline with heavy grazing across rangeland biomes of South Africa? More specifically, are responses in accordance with the generalized dynamic equilibrium model (grazing reversal hypothesis) of Milchunas et al. (1988) and May et al. (2009), for example, does species diversity or richness remain relatively constant or decline slightly with grazing in semi-arid areas with a long evolutionary history of grazing? In addition, what is the nature of species compositional change and species turnover with heavy grazing and how do changes in these, and in species richness, relate to the environmental gradients sampled?

2. Study areas

Arid and semi-arid rangeland areas of South Africa were systematically scanned using SPOT 5 satellite imagery for major vegetation contrasts that were deemed likely to have been caused by extensive land-use, mainly grazing intensity differences. Contrasts due to past cultivation were rejected. Thus candidate sample areas were selected from a systematically inspected zone with mean annual precipitation (MAP) less than 600 mm which makes up the large majority of the country. Extreme contrasts were sought as part of the pilot programme to first identify the most serious effects on biodiversity, and to increase the likelihood of including ecosystems that may have passed a degradation threshold with local species extinctions. Study areas (Fig. 1) were selected after careful ground checks to confirm land use history and ensure no discernible gradients in original environment or habitat across each contrast boundary fence line. Two of the selected study areas were in or immediately adjacent to the hyper-arid zone (Succulent Karoo and Kalahari dune savanna); two within the arid zone (Thicket and Nama-Karoo) and the remaining two in the zone classed as semi-arid (Grassland and Mopane savanna). Climatic zones follow Middleton and Thomas (1997) whereas biome divisions are after Mucina and Rutherford (2006). The last three mentioned study areas each constituted contrasts between commercial farms and heavily utilized communal land. The other three study areas represented contrasts between lightly and heavily stocked commercial rangeland farms. Savanna, which is the most extensive biome in South Africa, was represented by two study areas, each in two of the three main subdivisions ('Open *Acacia* of the southern Kalahari' and '*Colophospermum mopane* vegetation'; Werger and Coetzee, 1978) of the biome. For convenience, we list these two distinctive areas as 'biomes' in the context of the biome comparisons made below. Detailed descriptions of the study areas are available elsewhere (Rutherford and Powrie, 2010a, b, 2011; Rutherford et al., 2012a,b,c). Available records of stocking densities for study areas (Table 1) sometimes indicated only lower bounds of values.

Application of the grazing model requires categorization of length of evolutionary history of grazing for each study area. It should be noted that a global application of the model has shown that estimation of length of evolutionary history of grazing is 'necessarily subjective' (Milchunas and Lauenroth, 1993) and difficult, with a 'lack of hard evidence with good resolution' (Oesterheld and Semmartin, 2011). Nevertheless, given the firm indications of abundant pre-colonial

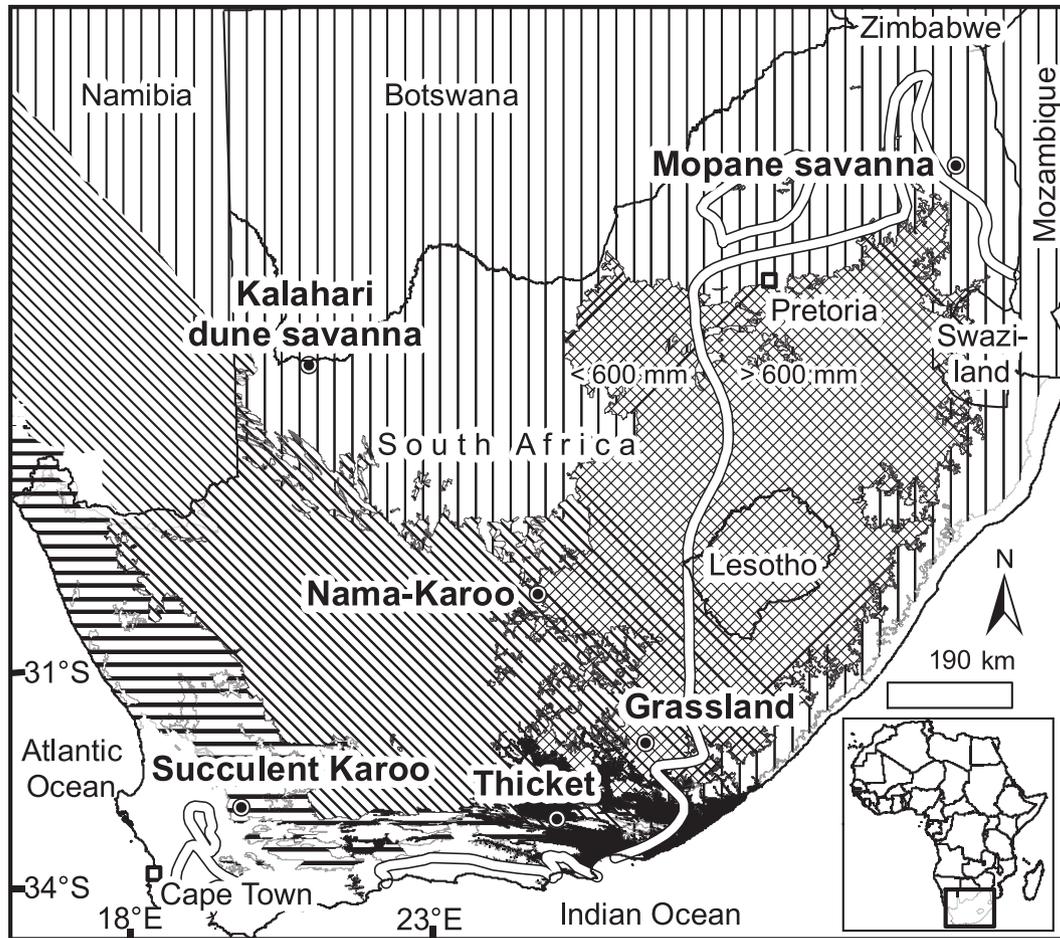


Fig. 1. Localities of study areas (circled dots) within their respective rangeland biomes. Two of the study areas are located in the Savanna biome. Non-rangeland biomes are not shown. The narrow white bands indicate the smoothed isohyets corresponding to a mean annual rainfall of 600 mm.

grazing ungulates in the savannas and grasslands of Africa (Stuart-Hill and Mentis, 1982; Owen-Smith and Danckwerts, 1997; Rutherford et al., 2006), and to some extent in the more grassy eastern Karoo (Dean and Milton, 2003) (Nama-Karoo biome), as well as high density elephant generalists in the Subtropical Thicket biome (Kerley and Landman, 2006), we assume a long evolutionary history of grazing or herbivory for these areas. The length of the evolutionary history of grazing in the Succulent Karoo biome seems less clear. With only apparent intermittent past occurrences of large herbivores in this biome (Dean

and Milton, 2003), Todd and Hoffman (2009) suggest that the biome has a short evolutionary history of grazing.

3. Methods

3.1. Approach

This paper focuses on site-level data and calculations relating to species heterogeneity are consistently based on data from pooled

Table 1
Biome study area characteristics and grazing treatments showing species heterogeneity indices that depend on relative abundances (cover) of species, and are based on pooled data per site. Study areas are in order of increasing mean annual precipitation.

Biome ^a	Vegetation type ^b	MAP (mm)	Stocking density (LSU ha ⁻¹)			Species diversity indices				Evenness indices			
			LU	HU	Ratio HU:LU	Shannon Wiener		Effective number of species		Pielou		Modified Hill ratio	
			LU	HU	Ratio HU:LU	LU	HU	LU	HU	LU	HU	LU	HU
Succulent Karoo	Tanqua Karoo	110	<0.020	0.042	>2.0	1.68	2.20	5.36	9.05	0.45	0.62	0.39	0.49
Kalahari dune savanna	Gordonia Duneveld	180	0.040	0.154	3.9	2.30	1.16	9.93	3.20	0.63	0.42	0.67	0.54
Thicket	Sundays Thicket	273	0.050	>0.090	>1.8	1.51	1.74	4.51	5.71	0.42	0.53	0.39	0.76
Nama-Karoo	Eastern/Northern Upper Karoo	352	0.055	>0.165	>3.0	1.30	1.79	3.68	6.01	0.32	0.43	0.57	0.71
Grassland	Queenstown Thornveld	480	0.130	≥0.620	≥4.8	2.49	2.07	12.07	7.95	0.57	0.47	0.59	0.50
Mopane savanna	Phalaborwa-Timbavati Mopaneveld	527	0.08–0.09	0.55–0.68	≥6.1	3.068	2.601	21.5	13.47	0.659	0.558	0.631	0.49

MAP: Mean Annual Precipitation

^a Includes two subdivisions of the Savanna biome.

^b According to [Mucina and Rutherford \(2006\)](#).

sample plots. As opposed to previously published calculations (Rutherford and Powrie, 2010a,b, 2011; Rutherford et al., 2012a,b,c) based on replicated individual sample plots, which are necessarily limited to plot scale, the pooled plots reflect species diversity and its components at the broader scale that represent each study site as a whole. This more comprehensive approach naturally provides descriptive statistics rather than statistical variance. Thus, for example, standard species abundance distributions provide important site-level information but are rarely subject to significance tests (McGill et al., 2007). It may be noted that, notwithstanding the above scale distinction, there was a significant positive linear relationship between mean diversity per sample plot and the diversity of the pooled data sets (Shannon–Wiener diversity: $n = 12$, $r = 0.91$, $p < 0.0001$).

Sampling layout consisted of randomly placed plots in equal number along both sides of the grazing contrast fence at a distance typically 15 m to 25 m from the fence to avoid possible fence-associated disturbance effects but also less than 50 m from the fence to maximise the probability of identical or near-identical prior conditions on both sides of the fence. Modified Whittaker plots were used for sampling in the first study undertaken, namely in Succulent Karoo (Rutherford and Powrie, 2010b), but were not applied at subsequent sites owing to the inefficiency of these relatively large and complex plots for detecting change. All other study areas used 50 m² sample plots except for the densely vegetated Thicket sites (Rutherford et al., 2012b) where smaller sample plots (9 m²) were needed for accurate area demarcation and reliable estimates of species canopy cover. The relatively lightly grazed reference side of the fence was referred to as low utilization (LU) and the heavily grazed side as high utilization (HU). LU and HU were regarded as two sites within each of the six study areas.

Every effort was made to record all vascular species and their estimated canopy cover within plots. Sampling was carried out at that time of year when most species, including annuals, were likely to be clearly present on a given study area. However, it should be noted that no single time of year is likely to be fully suitable for detecting all species on a site. Soil crusts were recorded where present and biological crusts were randomly sampled for herbarium identification of constituent moss (Bryophyta) and liverwort (Hepatophyta) species. These non-vascular plants were excluded from the plant species counts.

3.2. Use of species heterogeneity measures

Expressing diversity of systems has commonly been approached in two main ways, namely, those that include relative abundance or evenness of component elements or species, often with different weightings (e.g. species diversity indices), and those that address simply presence–absence of component elements or species (e.g. species richness). Both these abundance- and incidence-based approaches were followed, using plant canopy cover as a measure of abundance.

We calculated one of the most commonly used diversity indices, namely, the Shannon–Wiener diversity index (H') and its effective species number (Jost, 2006) for LU and HU on each study site (Krebs, 1989). The well-known Pielou evenness index was calculated as H' relative to maximum diversity for the species number at a site. Since, as indicated above, sample size differed between sites, we also calculated the modified Hill ratio as a measure of evenness as this index is generally insensitive to sample size (Alatalo, 1981; Beisel et al., 2003). In addition to these indices, we present the data in the form of species abundance distribution curves which are simple and effective for comparing diversity patterns, including their richness and evenness components, at site scale (Oldeland et al., 2010).

Species number or richness is a simple measure which has the major advantage over species diversity in allowing for different sample sizes by using standardized rarefaction curves. With species

richness, species weightings are irrelevant, and direct and unambiguous comparisons can be made between sites. Species area curves were derived using sample-based rarefaction curves (Mao Tau expected richness function in EstimateS 8.0, University of Connecticut, US), as described by Colwell et al. (2004). Results for each site thus ranged from the area of a single sample plot to the combined area of all the sample plots. The exponents (z) and coefficients (c) were determined from the commonly applied power curve (Dengler, 2009)

$$S = cA^z$$

where S is number of species and A is area measured in m². For the two Succulent Karoo sites power curves were obtained by regression with the scale-related data from the modified Whittaker plot data (both curves with $r > 0.99$). The exponent z is often quoted in diversity studies as 'slope' (Dumbrell et al., 2008) or 'rate of species accumulation' (Manne et al., 2007). However, the slope of a power curve is not a constant, and only in log–log space is the slope equal to the z -value (Desmet and Cowling, 2004). We nevertheless report explicitly on z and c following Gould (1979) and Lomolino (2001). We also calculated the actual slope as the derivative ($dS/dA = czA^{z-1}$) at $A = 250$ m² which was the maximum size sample area in common across all our study sites. The available methods of modelled estimates that extrapolate beyond incompletely sampled species richness were avoided, given the limitations in testing their assumptions (see Magnussen, 2011).

Species number or richness also permits use of overlap measures (Jost, 2006) for analyses of species turnover. We consider the following related elements of species turnover. The well-known Sørensen index (β_{sor}) has been used in various guises to express change in presence-absence data (Tuomisto, 2010) and constitutes a monotonic transformation of beta diversity (Baselga, 2012). Beta diversity is commonly regarded as reflecting turnover but also as the sum of replacement and richness differences (Carvalho et al., 2012) with the latter term variously interpreted as 'nestedness' (Almeida-Neto et al., 2012). Turnover through species replacement has commonly been given by the Simpson Dissimilarity Index (β_{sim}) (Baselga, 2012) and nestedness has been variously estimated, in one view, as the complement of β_{sim} . Thus the complement of β_{sim} with respect to the total on a given species-poorer sample site has provided NODF – Nestedness metric based on Overlap and Decreasing Fill (Almeida-Neto et al., 2012; Baselga, 2012). Alternatively, the complement of β_{sim} with respect to the Sørensen Dissimilarity Index has provided β_{sne} . We apply the latter parameter since it links clearly to the Sørensen Dissimilarity Index and remains valid where multiple site comparisons are not calculated (Baselga, 2012 – see also this reference for comparisons of β_{sne} and NODF). The relationships of the parameters calculated may be summarized as follows:

$$\beta_{sor} = (b + c)/(2a + b + c)$$

$$\beta_{sim} = \min(b, c)/(a + \min(b, c))$$

$$\beta_{sne} = \beta_{sor} - \beta_{sim}$$

where a is the number of species present in both sites, b is the number of species present in the first site but not in the second, and c is the number of species present in the second site, but not in the first. β_{sne} is the value determined by the richness difference 'conditioned by the degree of nestedness between sites' (Baselga, 2012). Although the interpretation of nestedness may be contentious, β_{sne} is nevertheless useful for determining how differences in species richness that are not due to species replacement contribute to patterns of beta-diversity along gradients (Almeida-Neto et al., 2012). It may be noted that use of the Sørensen indices is roughly equivalent to that of the other popular Jaccard family of indices (Baselga, 2012).

4. Results

Species data for each site are presented in the form of species abundance distributions in Fig. 2. The variation in species numbers is clearly evident with fewest species recorded on the HU site in Kalahari dune savanna and most species recorded in Mopane savanna. The species rarefaction curves (Fig. 3) also reflect the spread of data and indicate species richness expressed at the standardized maximum common area of 250 m². Species richness, at the standard area, in Mopane savanna and Succulent Karoo changed little with high utilization (<3% difference). However, species richness in Nama-Karoo and Grassland appeared to increase slightly (>10%) in contrast to the marked decreases in Thicket and Kalahari dune savanna (–27% and

–66% respectively). In terms of the rarefaction-generated confidence intervals, only the most extreme change in species richness, namely the decline in Kalahari dune savanna, was significant at $p < 0.05$. Changes in the curves' z-values with grazing were equivocal. The value declined for most study areas but showed a marked increase for the Kalahari dune savanna area. However, actual slope of the curve for Kalahari dune savanna declined with grazing (Table 2). The values of the coefficient c tended to vary inversely with the value of z.

There was only limited agreement between changes in species diversity and in species richness with heavy utilization (Tables 1, 2). In Kalahari dune savanna the decline in species diversity closely tracked that in species richness and in Nama-Karoo both species diversity and richness increased. However, in Mopane savanna and Grassland the

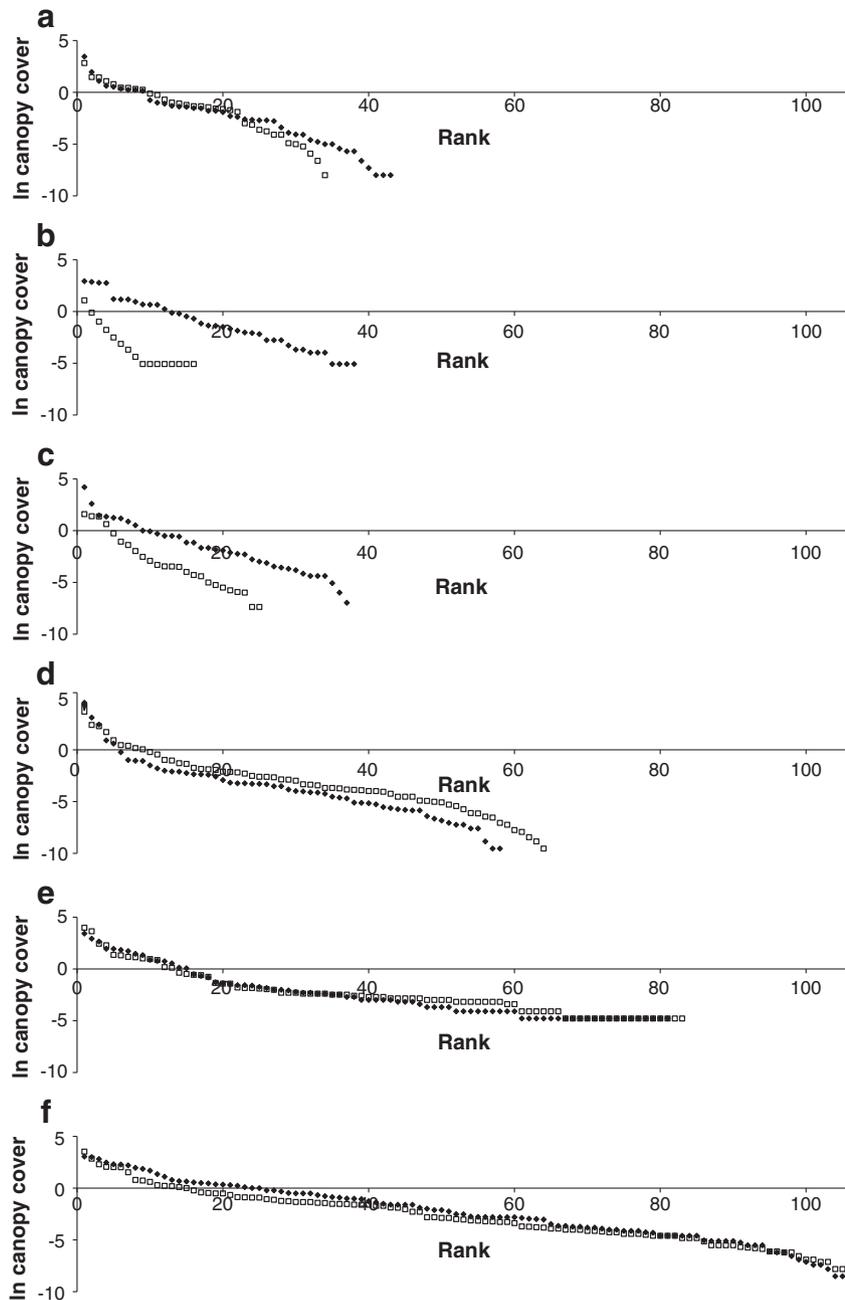


Fig. 2. Species abundance distributions for low utilization (LU – solid diamonds) and high utilization (HU – empty squares) on six study areas, using log base e. Study areas, in order of increasing mean annual precipitation, are: a) Succulent Karoo, b) Kalahari dune savanna, c) Thicket, d) Nama-Karoo, e) Grassland, and f) Mopane savanna. Recording precision of species cover was rounded to 0.1% for smallest plants on the Kalahari dune savanna and grassland study areas in contrast to 0.01% to 0.0002% on the other sites. Sample sizes and further detail in Rutherford and Powrie (2010a,b, 2011) and Rutherford et al., (2012a,b,c).

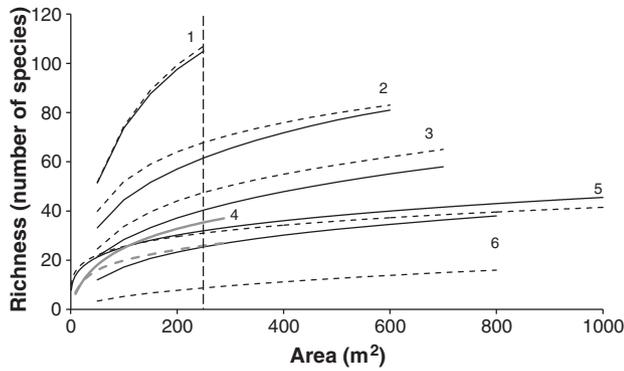


Fig. 3. Species area power curves over full sample size ranges for low utilization (LU – solid curves) and high utilization (HU – dashed curves) across biome sites based on sample-based rarefaction. Study areas are: 1) Mopane savanna, 2) Grassland, 3) Nama-Karoo, 4) Thicket, 5) Succulent Karoo, and 6) Kalahari dune savanna. The vertical dashed line represents the maximum sampling area (250 m²) in common with all study areas.

decline in species diversity did not correspond with the lack of decrease in their species richness. In Succulent Karoo the increase in species diversity did not agree with the slight decrease in species richness. For Thicket, the modest increase in species diversity contrasted with the second largest decline in species richness found with heavy utilization. All these discrepancies between species diversity and richness become more accentuated when only the more appropriate effective number of species is used as measure of species diversity (Table 1).

Changes in species diversity consistently followed changes in species evenness (Table 1) rather than richness. The evenness component of diversity appeared to outweigh the richness component in the case of each of the above mentioned discrepancies. Moreover, the greatest decline in species diversity, namely in Kalahari dune savanna, corresponded to large decreases in both species richness and species evenness (Tables 1, 2). Comparison between the four first-ranking species on LU and HU on the Kalahari dune savanna area illustrates the sharp change from relatively even to decidedly less even distribution for these species with heavy grazing (Fig. 2). The evenness indices of Pielou and the modified Hill ratio showed similar trends across the study areas.

Species richness at standard area showed clear trends along the rainfall gradient that was sampled. Species richness increased significantly with mean annual precipitation (MAP) for LU and for HU (Fig. 4). The magnitude of change in species richness across the rainfall gradient often greatly exceeded changes associated with heavy grazing at a site. The slight differences in the linear relationships for

LU and HU support the differences in the data which indicate a decline in species richness with heavy grazing for areas with MAP less than about 300 mm and an increase in richness for areas with MAP greater than about 300 mm.

The relative change in species richness was significantly related to loss of plant canopy cover. This curvilinear relation (Fig. 5), which starts appropriately at the origin, shows a slight increase in richness up to about 50% loss in canopy cover. With greater loss in canopy cover, but supported by data from only two study areas (Kalahari dune savanna and Thicket), a distinct loss in species richness is indicated. Thus species richness appears to remain relatively constant before a decline with increased grazing intensity, as measured by canopy cover loss.

Sørensen's dissimilarity index provides an indication of the turnover in species richness from LU to HU, and cannot itself be reliably predicted from the difference in species richness, as shown by Table 2. For example, almost no change in species richness corresponded with a dissimilarity index of 36% for Succulent Karoo versus a 10% change in species richness that corresponded with a 27% dissimilarity index for Grassland. The highest Sørensen's dissimilarity index, and hence apparent species turnover, was 69% for Thicket and lowest for Mopane savanna (22%). When the dissimilarity index is separated into its replacement and nestedness components only Kalahari dune savanna showed roughly equal contributions by both components (Fig. 6). The other study areas all showed strong dominance of species replacement over nestedness. There appeared to be no consistent relationship between MAP and species turnover (Table 2).

The proportion of annual plant species tended to increase moderately with heavy grazing on most sites, but with a particularly dramatic increase, by an order of magnitude, on the Thicket site (Fig. 7a). Although there was little change in the proportion of annual plant species for Succulent Karoo, the proportion of annual plant canopy cover more than doubled with heavy grazing on this site (Fig. 7b). The major overall change across the study areas was the large increase in cover of annual plants. Kalahari dune savanna was the exception where there was a strong persistence of larger woody perennials and low success in establishment of annual cover on the disturbed and destabilized dunes (see Rutherford and Powrie, 2010a). There appeared to be no consistent relationship between MAP and change in the proportion of annual species richness or cover (Fig. 7a, b).

Biological soil crusts were commonly recorded on LU usually consisting of blue-green algae but sometimes comprising a number of species of moss and liverwort. These biological crusts were usually destroyed on HU but sometimes replaced with weak physical soil crusts (Rutherford and Powrie, 2010a,b, 2011; Rutherford et al., 2012a,c). Alien plant species were rare on both LU and HU sites on

Table 2

Standardized species richness and properties of their species area power curves with low and high utilization intensities for biome study areas, in order of increasing mean annual precipitation.

Biome ^a	Species area power curve									Species richness at 250 m ²					β_{sor} (%)
	Exponent (z)			Coefficient (c)			Slope ^b			LU	SE	HU	SE	Diff.	
	LU	HU	Diff.	LU	HU	Diff.	LU	HU	Diff.						
Succulent Karoo	0.25	0.21	-0.04	7.83	9.73	1.90	0.033	0.026	-0.007	32.0	n/a	31.0	n/a	-1.0	36
Kalahari dune savanna	0.40	0.55	0.15	2.72	0.41	-2.31	0.039	0.019	-0.020	25.4	3.3	8.7	2.1	-16.7*	56
Thicket	0.48	0.35	-0.13	2.63	3.78	1.15	0.070	0.038	-0.033	35.3	3.9	25.9	3.8	-9.4	69
Nama-Karoo	0.37	0.36	-0.01	5.10	6.50	1.40	0.060	0.066	0.006	40.4	4.1	47.5	4.7	7.1	31
Grassland	0.35	0.28	-0.07	8.62	13.77	5.15	0.086	0.076	-0.010	61.6	4.5	67.8	4.6	6.3	27
Mopane savanna	0.45	0.46	0.01	9.18	8.86	-0.32	0.192	0.201	0.008	105.0	5.6	107.0	5.5	2.0	22

β_{sor} : Sørensen's dissimilarity index

Diff: Difference between LU and HU

SE: Standard error

^a Includes two subdivisions of the Savanna biome.

^b Calculated differential at 250 m².

* Significant at $p < 0.05$.

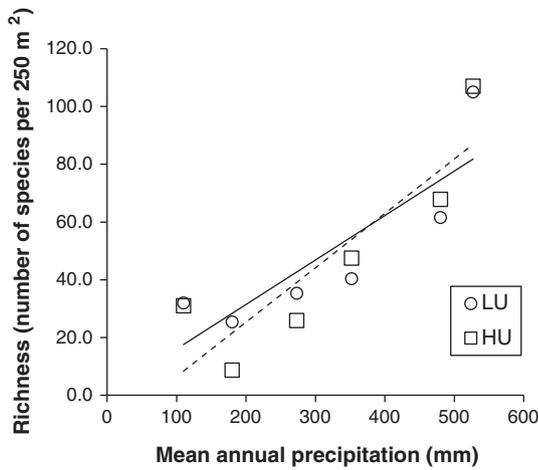


Fig. 4. Relationships between mean annual precipitation and species richness at 250 m² across biome study areas. The solid regression line is for low utilization (LU) with $r = 0.85$ and $p < 0.05$ and the dashed line for high utilization (HU) with $r = 0.88$ and $p < 0.05$.

all the study areas except on the heavily grazed Thicket site where alien plant species were relatively common (Rutherford and Powrie, 2010a,b, 2011; Rutherford et al., 2012a,b,c).

5. Discussion

The grazing responses found in this study only partly agreed with the predicted flat to slightly declining species richness of the generalized dynamic equilibrium model or grazing reversal hypothesis for semi-arid areas with a long evolutionary history of grazing (Milchunas et al., 1988; May et al., 2009). Discrepancies included the mildly positive increases in species richness found on the Nama-Karoo and Grassland study areas. More serious departures were the substantial declines in species richness found in Thicket and Kalahari dune savanna. The decline in species richness on these two last-mentioned study areas may be associated with particular conditions and warrants further consideration. Findings on species richness broadly agree with those of previous studies in thicket (Hoffman and Cowling, 1991; Lechmere-Oertel et al., 2005) and Succulent Karoo (Todd and Hoffman, 1999; Petersen et al., 2004; Allsopp et al., 2007; Anderson and Hoffman, 2007) and the lack of

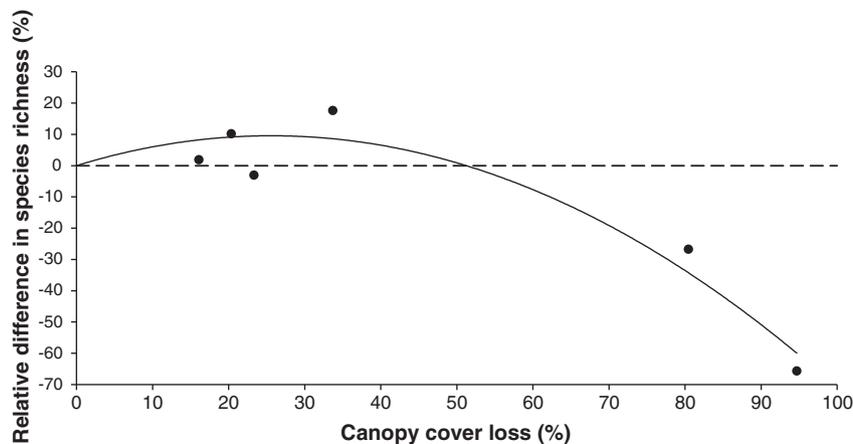


Fig. 5. Relationship trends across biome study areas between canopy cover loss and relative change (difference) in total species richness at 250 m² from LU to HU. The second degree polynomial regression is appropriately fitted through the origin, with $r = 0.96$ and $p < 0.005$. The dashed horizontal line represents zero change.

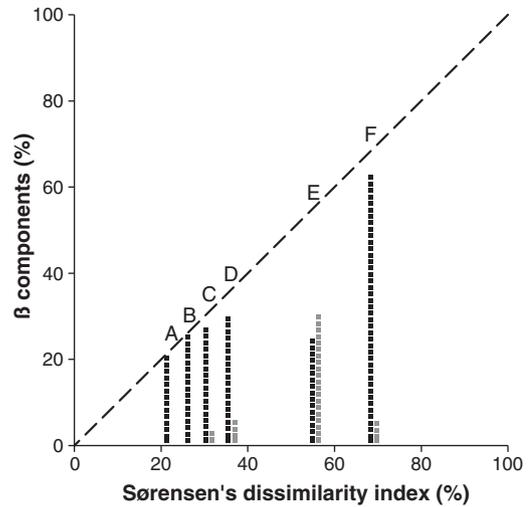


Fig. 6. Diagram showing the relative contributions of Simpson Dissimilarity Index (β_{sim}) and Beta nestedness (β_{sne}) to Sørensen's Dissimilarity Index across biome study areas. Study areas are: A) Mopane savanna, B) Grassland, C) Nama-Karoo, D) Succulent Karoo, E) Kalahari dune savanna, and F) Thicket. Dark bars represent β_{sim} and light bars β_{sne} . The dashed line shows the maximum limit of the summed beta components.

decline found for Mopane savanna accords with that in other savanna in the lowveld (Shackleton, 2000).

The greatest decline in species richness was on the Kalahari dune savanna site where grazing pressure apparently exceeded the threshold for substrate stability of the normally vegetated, fixed dunes. The species changes may thus not have been associated only with heavy grazing but also with the consequences of newly formed mobile dunes (Rutherford and Powrie, 2010a). Substrate destabilization is naturally not atypical of deleterious impacts in sandy arid environments. The second greatest decline in species richness was on the Thicket site which, although typical for the area, was remarkable in that it was overwhelmingly dominated by a single species, the succulent shrub *Portulacaria afra* Jacq., that formed most of the upper canopy and was highly palatable to local browsers (Rutherford et al., 2012b). The disappearance of this probable keystone species (see Ebenman and Jonsson, 2005) through high utilization may have led to the recorded collapse of many likely dependent species. There was nevertheless a significant replacement flora which, however, failed to balance the losses (Rutherford et al., 2012b). The grazing model does not appear to adequately account for the particular conditions above.

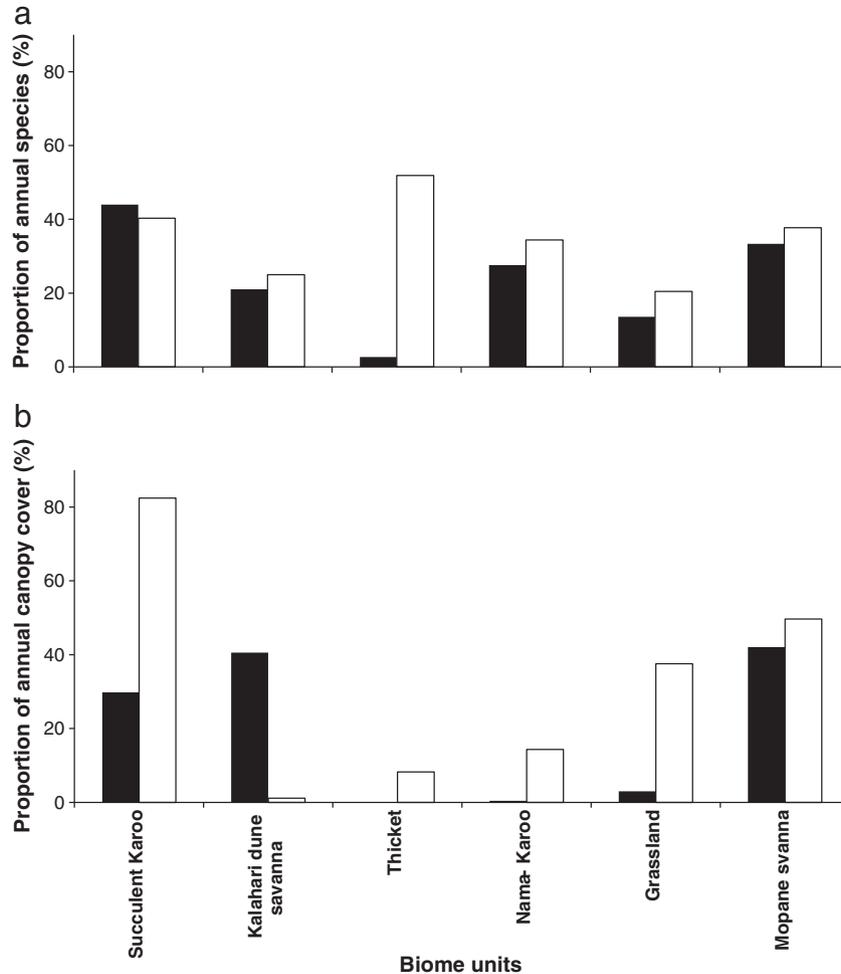


Fig. 7. Proportion of (a) annual species and (b) canopy cover of annual plants, for LU (solid columns) and HU (open columns) on biome study areas, in order of increasing mean annual precipitation.

If Succulent Karoo indeed has a short evolutionary history of grazing with greater sensitivity to grazing (Todd and Hoffman, 2009) the negligible change found in species richness at site level in this study and other studies (Todd and Hoffman, 1999; Petersen et al., 2004; Allsopp et al., 2007; Anderson and Hoffman, 2007) fails to match the substantial decline predicted by the model for such systems. It should be noted that the authors of the original model later emphasized (Oesterheld and Semmartin, 2011, Appendix S1) that the model describes four possible boundary or extreme cases and that continua forming a response surface between them may be expected.

Cingolani et al. (2005) have questioned the grazing model's assumption that only minor changes in floristic composition result with changes in grazing intensity in semi-arid communities with a long evolutionary history of grazing. The current study confirmed this reservation and found considerable compositional change mostly through substantial species turnover, due mainly to replacement of species. Even, irrespective of length of evolutionary history of grazing in areas that experienced very little change in species richness with grazing, namely, Succulent Karoo and Mopane savanna, species turnover was 36% and 22%, respectively. The availability of pools of grazing-resistant and less grazing-resistant species is critically important (Cingolani et al., 2005; Oesterheld and Semmartin, 2011) and is affected by the complex relationships between local and regional species richness (Harrison and Cornell, 2008). In the current study, only in Kalahari dune savanna did the relatively high species nestedness

component of the dissimilarity in species indicate a possibly significant limitation of suitable replacement species in the available pool. As pointed out by Cingolani et al. (2005), changes in species composition need to be taken into account in a modified version of the grazing model, especially for semi-arid communities with long evolutionary history of grazing.

Given the earlier-mentioned concerns regarding loss of species richness on heavily utilized communal areas, it is noteworthy that none of the three sites under communal use, namely, in Grassland, Nama-Karoo and Mopane savanna, recorded decreases in species richness with high utilization. This could support the contention that land degradation is not a necessary outcome of heavy communal grazing (Ward et al., 1998), depending on the definition of degradation used.

Although species richness may remain relatively constant with high utilization, the nature, quality and composition of the heavily grazed outcome is naturally of interest to many land users. On some sites the replacement flora is more characteristic of arid Karoo-like vegetation elements e.g. Thicket, Nama-Karoo and Grassland. More broadly there was an increase in the proportion of annuals on most sites but many of these are weedy, opportunistic, and widespread ruderals. Other evidence also strongly suggests declining palatability of plants with heavy grazing and hence further contributes to lower quality grazing for conventional domestic livestock (see Rutherford et al., 2012b). Long-term resilience to environmental perturbations of such grazed areas is not necessarily low (Vetter, 2009).

Although heavy grazing may not negatively impact species richness of vascular plant species on study areas in Mopane savanna and Succulent Karoo, inclusion of the strongly negatively impacted bryophyte and liverwort species of the biological soil crusts in these systems, could well result in an overall negative impact on species richness measures that include macrophytic lower plants. However, it also appears that such negative impacts need not necessarily be long-lasting. A relatively rapid recovery of biological soil crusts, that included mosses, was found following livestock exclusion within a dryland region of Australia (Read et al., 2011).

A particularly interesting finding of this study was that the magnitude of change in species richness across the relatively limited rainfall gradient often greatly exceeded changes associated with heavy grazing at a site (Fig. 4). In other words, site location can be far more important in determining plant species richness than heavy grazing or high utilization. What makes this remarkable is to recall that all the study areas were specifically selected for their probable major grazing impact in each region. These extreme cases nevertheless appear to confirm patterns of a global analysis in which 'the predominance of ecosystem-environmental variables rather than grazing variables in sensitivity analyses suggests that where we graze may be more important than how we graze' (Milchunas and Lauenroth, 1993). Species richness was found to be greater for winter rainfall areas than for summer rainfall areas of similar MAP in the west of the subcontinent (Schmiedel et al., 2010). This may explain the relatively elevated species richness position of our winter rainfall study area of the Succulent Karoo (with lowest MAP) relative to that indicated by other summer rainfall study areas with relatively low MAP in Fig. 4.

The non-equilibrium persistent model assumes that the high variability, in e.g. rainfall, in more arid areas results in plant and herbivore populations being driven mainly by climatic factors with only a small role for biological interactions, including herbivory (Fernandez-Gimenez and Allen-Diaz, 1999). The expected limited effect of grazing on plant species richness in arid areas is, however, clearly not well supported by the results of our study. Although our results do indicate that mean annual rainfall can be more important in determining plant species richness than heavy grazing, other studies have shown that the ecosystem response to rainfall and grazing is complex (Fernandez-Gimenez and Allen-Diaz, 1999). A study in semi-arid savanna in the Pongola region of South Africa clearly contradicted the notion that semi-arid African savannas are non-equilibrium systems in which rainfall overrides grazing (Fynn and O'Connor, 2000). More recently, there is a growing recognition that most rangelands show elements of both equilibrium and non-equilibrium dynamics (Todd and Hoffman, 2009).

Although the relationship between canopy cover loss and change in species richness is intuitively appealing and statistically significant (Fig. 5), it is strongly influenced by data from the two study areas with maximum decline in species richness, which were linked to specific conditions described above. This relationship nevertheless has much potential for extensive spatial application of changes in species richness using remote sensing data on canopy cover change and needs to be further explored and expanded. Determining and mapping the necessary baseline species richness across biomes in the subcontinent using, for example, soil properties (see Medinski et al., 2010), may prove equally challenging.

The rarefaction species-area power curves have been shown to be most advantageous in comparing species richness for different spatial scales and sample sizes. The interpretation of the oft-quoted exponents (z) of such power relations appears less certain. In the current study, the values of z at specified standard area declined on four study areas with heavy grazing in accordance with the expectation that disturbance tends to decrease the value of z (Dumbrell et al., 2008). However, there was a strongly opposite effect in Kalahari dune savanna where z increased to the high value of 0.5 on HU (Table 2), which falls beyond the typical range of 0.1 to 0.4

(Lomolino, 2001) or 0.5 (Lomolino, 2000). Data from this study area also demonstrate how z as an indicator of slope (Schmiedel et al., 2010) is unreliable when compared to calculated actual slopes (Table 2). The exponent z is not independent of the coefficient c and can in this study be seen to relate inversely to the coefficient c (Table 2). There is a need to further explore the biologically relevant variation in c -values as they combine with z -values to determine slope (Lomolino, 2001). It should be noted that it has been shown that there are important other specific applications of z where only proportions of areas or species are of concern and where the coefficient c can consequently be ignored (Desmet and Cowling, 2004).

That species evenness decreased on half our study sites but increased on the others parallels the variable response found in evenness in a relatively small global data set with disturbance that included grazing, although negative responses were found to be more frequent (Mackey and Currie, 2001). Our observed changes in evenness indicated an interesting pattern. The initially low evenness values increased with heavy grazing whereas the initially high evenness values decreased. This is well exemplified by the Pielou evenness indices in areas with values under 0.5 which increased to values above 0.5 with grazing and conversely those initially above 0.5 which dropped to below 0.5 with grazing. Changes in evenness may thus depend on initial condition. With values constrained between 0 and 1, the probability of evenness becoming less extreme may be greater than the probability of becoming more extreme, thus exhibiting a central tendency pattern.

Results clearly show that species evenness can have a strong effect on species diversity indices which can outweigh the species richness component of diversity, as has been reported elsewhere (Stirling and Wilsey, 2001). In our study, plant canopy cover was the measure of abundance used to determine species evenness. Plant canopy cover is directly and immediately sensitive to grazing, so that its influence through evenness on diversity indices can also be immediate and can quickly mask any changes in richness. It has been stated, more generally, that evenness responds more rapidly to human activities or altered environmental constraints than richness, i.e. respond more rapidly before species become extinct (Hillebrand et al., 2008).

This study has used plant species as the primary concept unit of diversity and richness. More recently there have been increasing references to shifts away from a focus on species in biodiversity studies (O'Connor and Kuyler, 2009) with trait diversity and functional types being put forward as alternatives to species diversity (Mayfield et al., 2010). However, species diversity remains 'the most commonly used indicator of biodiversity' (van Wieren and Bakker, 2008) and is 'strongly positively correlated with diversity at other levels or organization, such as genetic diversity and ecosystem functioning' (Chiarucci et al., 2011). Until such time that a comprehensive, workable and accepted alternative functional classification of plants becomes established, we think that the species level expression of diversity and richness remains a viable practical option for comparative studies. We do acknowledge that the problem of comprehensive species assessments is often not trivial. The challenges of meeting the effort and cost of detecting all species with the particular difficulties regarding the uncommon species remain (see O'Connor et al., 2011). Continuing emphasis on species as biodiversity elements relies heavily on effective taxonomic identification services underpinned by active taxonomic revision and research, and is particularly important in a developing and bio-diverse country such as South Africa.

The novel species richness comparisons and analyses of this report have been based on original data and certain findings abstracted and developed from previous studies described in the hexalogy (Rutherford and Powrie, 2010a,b, 2011; Rutherford et al., 2012a,b,c). The present paper is certainly not a full synthesis of the previous works and substantial other relevant material remains to be found in these individual studies, which include details on plot-level diversity,

individual plant species reactions, growth forms, vegetation structure and soil properties.

6. Conclusions

This study has shown that heavy grazing need not necessarily lead to reduced plant species richness. On some sites even a modest increase may be indicated whereas the few large decreases may be associated with special secondary conditions that may occur in arid areas. Relative to the magnitude of changes in species richness across the rainfall gradient in arid and semi-arid South Africa, heavy grazing appears to often have a relatively minor effect. Indeed, as stated over two decades ago, overgrazing may be overstated (Mace, 1991). However, heavy grazing changed composition and often adversely affected quality and favoured annual species but with alien species making up surprisingly few of the replacement species on most study areas.

The study confirms that plant species diversity, as expressed by commonly used indices, is a relatively complex measure which does not reliably reflect its species richness component. Evenness can have a dominant effect and result in diversity measures obscuring important trends and patterns in species richness. Sole use of measures of diversity, without its components, can therefore be ambiguous.

The current work remains distinctly limited in the range of conditions that have been studied, and has also avoided the sub-humid regions. While the availability of an anticipated national map of degradation (Driver et al., 2012) will represent an advance, understanding the consequences of degradation for biodiversity across the whole country will require much more widely directed, yet detailed investigation. Some of our results imply that biodiversity may be very little affected by heavy grazing in some areas and these results should be noted by policy makers. However, we believe that further work is needed in a multidisciplinary context before concrete recommendations can be made regarding, for example, possible changes to destocking policies. Given the great diversity of types of environmental disturbance and degradation, as well as local biotic, environmental and historical idiosyncrasies, contingency may well be shown to limit capacity to predict or model outcomes (see Scheiner and Willig, 2008). Ecological understanding, let alone prediction, is inseparable from issues of contingency, historicity, uniqueness and complexity that continue to characterize ecology (Price and Billick, 2011).

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