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Long-term dynamics of herbaceous vegetation structure and composition in two African savanna reserves

Robert Buitenwerf[1]*, Anthony M. Swemmer[1] and Mike J.S. Peel[2]

[1]SAEON Ndlovu Node, Private Bag X1020, Phalaborwa 1390, South Africa; and [2]Agricultural Research Council, Animal Production Institute, PO Box 7063, Nelspruit 1200, South Africa

Summary

1. Small fenced reserves are perceived to require management interventions to maintain ecosystems in a natural state. Such interventions are typically initiated and assessed on the basis of short-term observations, while slow changes are often misunderstood or missed entirely. Long-term monitoring is therefore crucial to understand the effect of reserve management on ecosystem structure and functioning.

2. We analysed a 15-year data set of herbaceous vegetation data for 59 monitoring sites in two nature reserves of different size and with different management regimes in a semi-arid, South African savanna. Community composition and vegetation structure (basal cover) were assessed in response to rainfall and management variables.

3. No directional changes over time were found. Basal cover as measured by two proxies (distance to the nearest tuft and tuft diameter) increased with current and previous year rainfall. The relative abundance of functional groups also responded to rainfall, with perennial grasses increasing in relative abundance following a wet year. Compositional responses, as measured by a dissimilarity index of species relative abundance, showed a 2-year lag and responses were larger following dry years than wet years.

4. The response to rainfall of distance to the nearest tuft was significantly weaker in the smaller reserve, while compositional change during dry years was larger than in the larger reserve.

5. *Synthesis and applications*. Most of the variation in herbaceous basal cover and community composition was associated with differences between years (time) at each site, rather than with differences between sites (space), indicating that inter-annual variation in rainfall is the most important driver of herbaceous layer dynamics in these systems. However, management did modify the effects of rainfall on herbaceous structure and community composition. The smaller reserve, which had higher grazer and waterhole density, showed greater fluctuations in key herbaceous variables. Such reserves are common in southern Africa and probably require more careful management than larger reserves in the face of global climate change.

Key-words: basal cover, Bray–Curtis dissimilarity, climate change, Kruger National Park, mixed-effects model, reserve management, South Africa, vegetation dynamics

Introduction

Savannas are one of the most extensive terrestrial biomes, covering about 50% of Africa. Globally 12–13% of savannas are formally protected by IUCN standards and much of the rich biodiversity of African savannas, including most large mammals, now persist primarily within protected areas (Chape *et al.* 2005; Newmark 2008). However, in southern Africa many protected savanna ecosystems (typically called 'game reserves') exist as small fragments, fenced off from the larger ecosystems they were once part of and often surrounded by pastoral land or human settlements (Chape *et al.* 2005; Newmark 2008). While these fragments are considered to be 'protected', the integrity and persistence of their biodiversity depends on the effects of their relatively small size and isolation on ecological processes. Such effects can be negative in terms of primary and secondary productivity (Boone & Hobbs 2004; Owen-Smith 2004; Boone *et al.* 2005; Fryxell *et al.* 2005; Searle, Hobbs & Jaronski 2010). Furthermore, substantial management actions are often initiated in these reserves in an

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*Correspondence author. E-mail: buitenwerfrobert@hotmail.com

attempt to mitigate the effects of fragmentation that are perceived to be adverse, to recreate ecological conditions perceived to occur in larger, more 'natural' protected areas or to improve economic gains from eco-tourism or hunting ventures. A typical example is the creation of artificial waterholes, which are intended to increase the populations of large mammals and improve game viewing. The long-term consequences of such management actions coupled with fragmentation, are rarely investigated despite widespread perceptions that land degradation is far more common in smaller protected areas (Owen-Smith 2004; Peel, Kruger & Zacharias 2005). While ecosystem responses to these interventions may take decades to become apparent, reserve managers typically assess changes over more tangible time periods (often one to a few years). The full extent of changes caused by management interventions is therefore often misunderstood, or missed entirely. Long-term monitoring is thus crucial for the successful management of ecosystems, particularly in small reserves. Moreover, in many savanna regions inter-annual rainfall variability is high and drives annual changes in vegetation structure, production and even composition (Rutherford 1980; Deshmukh 1984; Le Houerou 1984; O'Connor 1985; Gibson & Hulbert 1987; Lauenroth & Sala 1992; Illius & O'Connor 1999; Anderson & Inouye 2001; Fuhlendorf, Briske & Smeins 2001; Knapp & Smith 2001; Swemmer, Knapp & Snyman 2007). This makes it difficult to detect trends over periods of only a few years, making long-term data even more valuable for analysing these systems.

We used 15 years of data from a South African semi-arid savanna on the structure and composition of the herbaceous vegetation to compare two reserves that differ both in size and in a range of management interventions that are typically applied in southern African savanna reserves. While there is a wide range of ecological variables that may respond to differences in reserve management, we have selected the structure and composition of the herbaceous vegetation for three reasons. First, these were the only variables for which a long enough time series was available to capture slow responses that may take many years or decades to manifest.

Secondly, the structure and composition of the herbaceous layer provides an index for a whole suite of ecological functions. A key measure of herbaceous structure is basal cover, which is a primary indicator of ecosystem functioning (Snyman 1998; Ludwig *et al.* 2005). Basal cover is positively related to above- and below-ground phytomass production and soil N concentrations (Snyman 2005, 2009) while high basal cover reduces water run-off and evaporation (Ludwig *et al.* 1999; Snyman & du Preez 2005) and promotes infiltration (Knoop & Walker 1985; O'Connor, Haines & Snyman 2001). Community composition can also strongly affect primary productivity (Milchunas & Lauenroth 1993; O'Connor, Haines & Snyman 2001; Tilman *et al.* 2001), and forage palatability for grazers. Since certain species have the potential to form larger tufts than others, community composition is also related to basal cover (Allen, Wilson & Mason 1995).

Thirdly, the structure and composition of the herbaceous layer are some of few ecological variables that are amenable to manipulation in response to management actions, at least in smaller reserves. Managers may alter the herbaceous layer by applying different burning regimes, by altering the stocking rates of grazers, either directly or through the provision of artificial water points or by removing trees (bush clearing). Both fire and grazing are known to have a strong impact on the herbaceous layer in semi-arid ecosystems (Kelly & Walker 1976; Milchunas & Lauenroth 1993; Illius & O'Connor 1999; Snyman 2004; Zimmermann *et al.* 2008).

Of the two reserves, one was smaller, fully fenced, and had a higher density of artificial water points and grazing herbivores. We expected that on this reserve grazing would be more homogeneous across the reserves, resulting in over-grazing during dry years when grass productivity was lower. We therefore hypothesize that the smaller reserve would show a degradation trend over the study period, evident as a decline in basal cover, a decline in the abundance of perennial grasses, and greater inter-annual variation in grass community composition (as a result of an increased abundance of annual grasses, which vary more in density from year to year than perennial grasses). As rainfall is a primary driver of the herbaceous layer in these systems (Rutherford 1980; O'Connor 1985) we included the effects of annual rainfall, and investigate whether differences in management regimes override natural variability that arises from variability in rainfall.

Materials and methods

STUDY SITES

Monitoring sites were located in two adjacent, privately owned reserves: Klaserie Private Nature Reserve and Umhlametsi Conservancy, located in a low-altitude, semi-arid savanna region in eastern South Africa (−24·04°S to −24·36°S and 30·95°E to 31·32°E). The parent geological material in both reserves consists mainly of granites and granite–gneisses, with relatively sandy and infertile soils (Witkowski 1983). The woody vegetation is composed of *Acacia nigrescens*, *Colophospermum mopane* and *Combretum apiculatum* open woodland (Witkowski & O'Connor 1996; Peel, Kruger & MacFadyen 2007). There are no distinct herbaceous vegetation types (Witkowski 1983) although topo-edaphic gradients do exist (Venter 1986).

The climate is semi-arid with a mean annual rainfall of 443 mm over the last 32 years. A distinct wet season between October and April is also the growing season for plants. Annual rainfall (July–June) over the study period ranged from 218 to 876 mm (Appendix S1, Supporting Information). The average of five rainfall recording stations within the two reserves was used (max. distance between stations was 35 km).

The two reserves have very different management histories, and between them incorporate most of the management practices used on private conservation areas in the region. Reserve-specific characteristics are shown in Table 1. Klaserie had a lower density of artificial water points, lower tree canopy cover and a lower density of grazers. The much lower density of mixed feeders on Umhlametsi reflects the absence of elephants *Loxodonta africana*. In Klaserie half of the sites were burned once over the past 23 years while in Umhlametsi no fires were recorded over the study period. Fire was therefore excluded as a predictor variable.

Table 1. Environmental characteristics of the two reserves studied

	Klaserie Private Nature Reserve	Umhlametsi Conservancy
Area (km^{-2})	587·7	79·1
Fencing	No fence along eastern boundary*	Fully fenced
No. waterholes km^{-2}	0·20	0·34
Tree canopy cover (per cent, mean ± SE)	28·8 ± 0·7	37·2 ± 1·2
Herbivore density (kg ha^{-2}, mean ± SE)†		
Bulk grazers	1525 ± 145	1625 ± 148
Selective grazers	104 ± 21	710 ± 77
Mixed feeders	2270 ± 206	500 ± 53
Browsers	530 ± 31	1863 ± 174
Elephants present	Yes	No

*This connects the reserve to the Greater Kruger National Park (± 20 000 km^{-2}).

†Calculated from annual aerial game counts in Klaserie (14 years) and Umhlametsi (12 years).

MONITORING

A total of 59 monitoring transects were established in the study reserves by the Agricultural Research Council of South Africa (33 in Klaserie and 26 in Umhlametsi), as part of a research programme designed to advise land owners on natural resource management. Annual data from 1993 until 2007 were analysed, incorporating over 63 000 individual measurements. Some years are missing due to the fencing out of some sites (Appendix S1, Supporting information). The herbaceous vegetation was sampled using the nearest plant method (Foran, Tainton & de Booysen 1978) on a 100 m line transect that was laid out as a square with 25 m sides. At every metre the closest herbaceous tuft was identified to species level for grasses, yielding relative abundance of each species. Herbaceous dicotyledons were not identified to species and were grouped as 'forbs'. Similarly, species belonging to the Cyperaceae family were grouped as 'sedges'. To estimate basal cover (i.e. the proportion of ground covered by herbaceous plant material at ground level), the nearest plant method was combined with the distance method (Hardy & Tainton 1993) in which the distance from the transect measurement point to the closest tuft and the tuft diameter are measured. A commonly used formula for combining distance to tuft and tuft diameter into a single measure of basal cover (Hardy & Tainton 1993) was found to be inaccurate and unreliable for the communities involved in this study (data not shown), as were other simple indexes combining these two variables (such as tuft diameter/tuft distance). Tuft diameter and distance to tuft were therefore analysed separately as proxies for basal cover. A tuft was defined as a continuous unit at ground level, so that a fragmented individual may consist of multiple tufts. Distance to tuft was measured to the edge of the tuft that was nearest to the transect point. The same three observers took both measurements throughout the study, and observer bias was minimal.

ANALYSIS

To test community changes at a functional group level, herbaceous plants were grouped into forbs, perennial grasses and annual grasses. This is a grouping commonly used by managers in the region, and reflects general differences in key grazing variables such as forage production and forage quality (Tainton 1999).

To assess species-level compositional change we condensed species relative abundances into a dissimilarity matrix using the Bray–Curtis dissimilarity index in the vegan package (Oksanen *et al.* 2009) for R (R Development Core Team 2009). Community dissimilarity values between pairs of consecutive years were extracted for every site. With the chosen sampling effort it is likely that the relative abundance of rare species is underestimated and therefore we omitted species with a total relative abundance $<0{\cdot}5\%$ from the analysis. Changes in the abundance of individual species were not analysed, as the relative abundances of even the most common species in this study were highly variable between years and are therefore potentially unreliable predictors of absolute abundances.

Since classical repeated measures ANOVA is not well suited to analyse unbalanced designs with missing data (Bolker *et al.* 2009), we analysed each response variable with a linear mixed-effects model (LME) in the nlme package (Pinheiro *et al.* 2009) for R (R Development Core Team 2009). The parameters are estimated by maximum likelihood which is not affected by unbalanced or missing data (Pinheiro & Bates 2000). Model selection was performed by constructing a full model in which all fixed predictor variables were present and subsequently removing non-significant ($P > 0{\cdot}05$) terms. Significance of fixed terms was determined with conditional F-tests (Pinheiro & Bates 2000). The final, best fitting, model was then refitted using REML as suggested by Pinheiro & Bates (2000) to obtain unbiased coefficients and confidence intervals.

The fixed predictor variables included in the models were year (continuous), the current year's rainfall (continuous), the previous year's rainfall (continuous), reserve (categorical), mean tuft diameter per site in the previous year (continuous) and mean tuft distance per site in the previous year (continuous). Given the non-normal distribution of the data, we used the geometric mean for tuft distance and tuft diameter. Tuft diameter and distance to tuft were not correlated. We checked for collinearity between predictor variables with the tolerance value (Quinn & Keough 2003). Tolerance was $>0{\cdot}9$ in all cases, indicating no significant collinearity. We included site as a random factor allowing the errors of the repeated measures within a site to be correlated. To meet the model assumptions of normally distributed errors we log-transformed the response variables tuft diameter and distance to tuft. Dissimilarity and the proportion of perennial grasses were not transformed.

Results

TIME TRENDS

No time trends were found for any of the response variables, i.e. adding year as a predictor variable did not improve model fit for tuft diameter, distance to tuft, community dissimilarity and the relative abundance of functional groups. There were also no significant time trends for the relative abundance of individual species (data not shown).

TUFT DIAMETER

Tuft diameter was best explained by a model including reserve, rainfall in the previous year and tuft diameter in the previous year, including main effects and one 2-way interaction: *rainfall of the previous year × diameter in the previous year* ($F_{1,450} = 16{\cdot}6$, $P < 0{\cdot}001$). Tuft diameter increased with increased rainfall of the previous year and this effect was enhanced by increased tuft diameter in the previous year (Fig. 1).

Of the total variation in tuft diameter 31% was attributable to differences between sites of which 24% was associated with the predictor variables. The remaining 69% of total variation was ascribed to the repeated measures within sites, of which 39% was attributable to the predictor variables (Table 2).

DISTANCE TO TUFT

Distance to tuft was best explained by a model that included reserve, current year rainfall and distance to tuft in the previous year, with significant two-way interactions *current year rainfall* × *reserve* ($F_{1,497} = 10{\cdot}1$, $P < 0{\cdot}01$) and *current year rainfall* × *tuft distance in the previous year* ($F_{1,497} = 21{\cdot}5$, $P < 0{\cdot}0001$), and a marginally significant *reserve* × *tuft distance in the previous year* interaction ($F_{1,497} = 3{\cdot}8$, $P = 0{\cdot}051$). Large distances to tuft in the previous year resulted in large distances to tuft in the current year and this effect became more pronounced at low rainfall (Fig. 2). However, as rainfall increased the effect of previous year distance to tuft diminished and disappeared entirely when rainfall was above average. This effect differed between reserves, with more than ±750 mm rainfall required to overcome the effects of previous year's distance in Umhlametsi, but only ±600 mm required in Klaserie.

The total variation in distance to tuft that was attributable to differences between sites was 12% of which 52% was associated with predictor variables. The remaining 88% of total variation was ascribed to the repeated measures within site, of which 36% was associated with the predictor variables (Table 2).

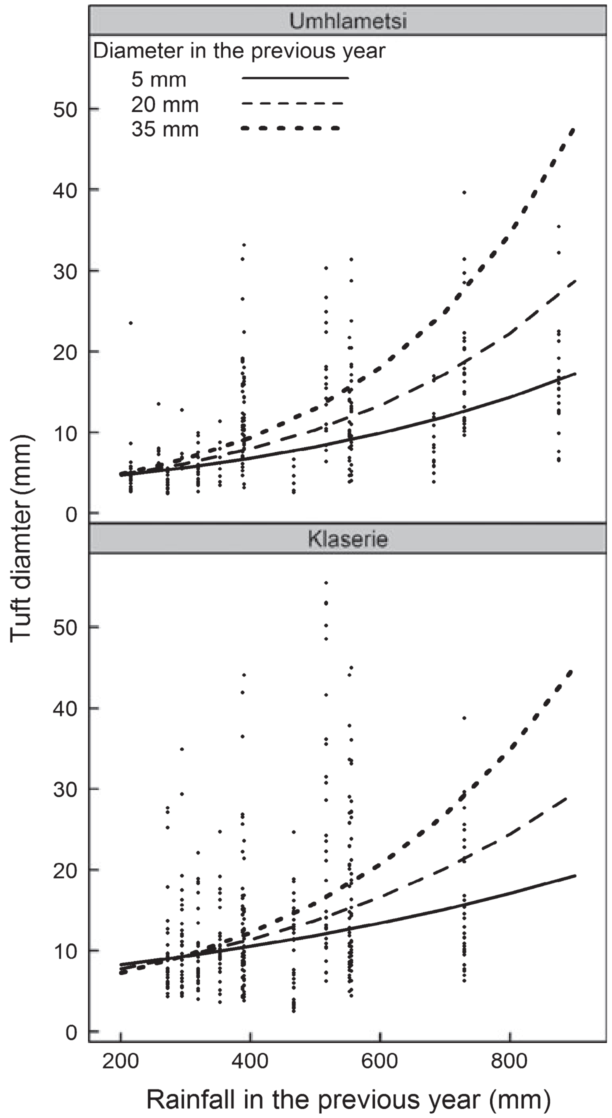

Fig. 1. Tuft diameter vs. rainfall of the previous year for both reserves. Superimposed lines are linear mixed-model predictions for arbitrarily selected tuft diameters in the previous year.

COMMUNITY COMPOSITION

The relative abundance of each functional group did not differ significantly between the two reserves (perennial grasses: $F_{1,58} = 2{\cdot}1$, $P = 0{\cdot}16$; annual grasses: $F_{1,58} = 1{\cdot}2$, $P = 0{\cdot}28$; forbs: $F_{1,58} = 1{\cdot}4$, $P = 0{\cdot}24$).

The relative abundance of perennial grasses increased drastically in years following a wet year ($F_{1,500} = 322{\cdot}3$, $P < 0{\cdot}0001$) (Fig. 3). This happened equally in both reserves. The relative abundance of perennial grasses was also positively related to the proportion of perennial grasses in the previous year ($F_{1,500} = 190{\cdot}1$, $P < 0{\cdot}0001$). Forty per cent of the total variation was attributed to differences between sites of which 64% was associated with predictor variables. The remaining 60% of total variation was ascribed to repeated measures within sites, of which 45% was associated with the predictor variables (Table 2). The most abundant perennial grasses were *Urochloa mosambicensis* (Hack.) Dandy, *Panicum maximum* Jacq., *Digitaria eriantha* Steud. and *Schmidtia pappophoroides* Steud. ex J.A. Schmidt and together made up 29·5% of overall relative abundance. The increase in palatable grasses after a wet year was accompanied by a decrease in the abundance of forbs (overall relative abundance = 23·3%) and annuals [*Brachiaria deflexa* (Schumach.) C.E. Hobbs ex Robyns and *Tragus berteronianus* Schult. were the most common, and together made up 15% of overall relative abundance]. Perennial grasses had on average significantly larger tufts (34·8 ± 0·20 mm) than annual grasses (13·6 ± 0·12 mm) and forbs (16·0 ± 0·43).

There was a lag in the response of community composition to rainfall. Compositional change as measured by Bray–Curtis dissimilarity decreased sharply with increasing rainfall of the previous year (Fig. 4), i.e. when rainfall in year one was high, compositional change between year two and year three was small. Again, this effect differed for the two reserves ($F_{1,500} = 8{\cdot}1$, $P < 0{\cdot}01$). Conditional *t*-tests from the LME model show that while the effect of previous year rainfall on compositional change was highly significant in Umhlametsi ($t_{500} = -6{\cdot}8$, $P < 0{\cdot}0001$), it was absent in Klaserie ($t_{500} = 0{\cdot}73$, $P = 0{\cdot}46$).

Table 2. Statistical details of linear mixed-model

Response variable	Btw var (%)	Wth var (%)	Model term	*F*	*P*
Tuft diameter	31·1 (23·7)	68·9 (38·9)	reserve	17·7	***
			prev rain	236·4	****
			prev diam	10·2	**
			prev rain × prev diam	16·6	**
Distance to tuft	12·0 (51·8)	88·0 (36·2)	reserve	11·2	**
			curr rain	203·6	****
			prev dist	42·2	****
			reserve × curr rain	10·0	**
			curr rain × prev dist	21·6	****
			reserve × prev dist	3·7	0·05
Proportion perennial grass	39·6 (63·7)	60·4 (45·4)	prev rain	322·3	****
			prev prop perennial	190·1	****

Only the significant or nearly significant model terms are displayed. Significance of *P* values: * < 0·05, ** < 0·01, *** < 0·001, **** < 0·0001.

Btw var, between group variance, where group is a plot in a certain year; Wth var, within group variance.

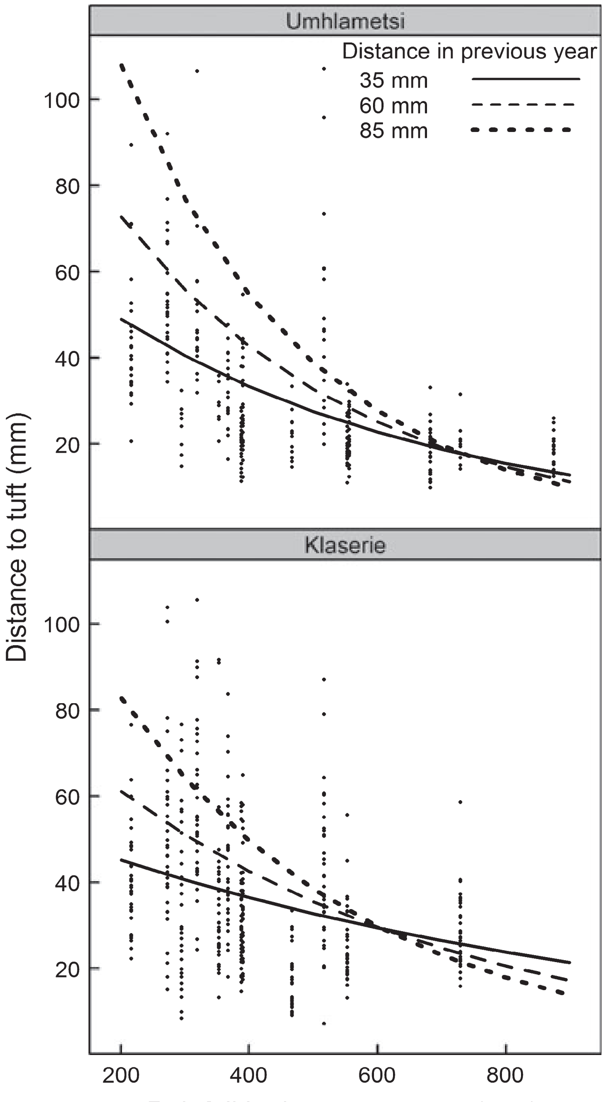

Fig. 2. Distance to tuft vs. current year rainfall for both reserves. Superimposed lines are linear mixed-model predictions for arbitrarily selected distances to tuft in the previous year.

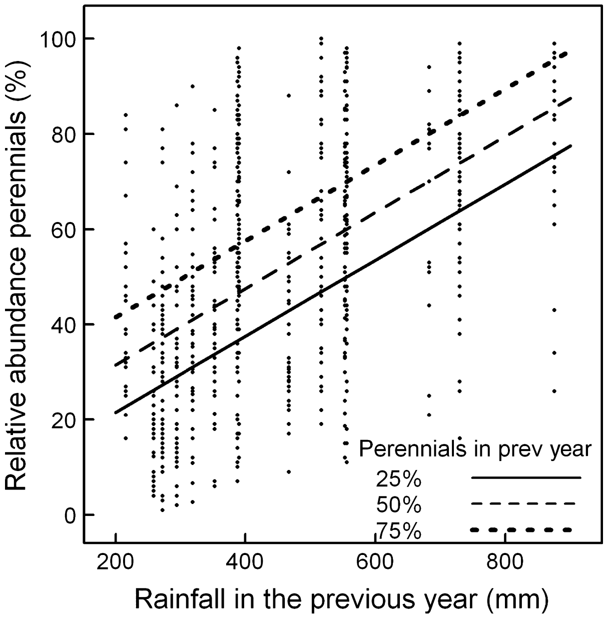

Fig. 3. Relative abundance of perennial grasses vs. annual rainfall of the previous year. Lines are predictions from the linear mixed-model for arbitrarily selected relative abundances of perennial grasses in the previous year.

Discussion

Although the data analysed were collected for short-term management purposes, they provide useful insights into long-term effects of different management strategies, which are employed on reserves throughout southern Africa, and elsewhere. The proxies of basal cover (tuft diameter and distance to tuft) and community composition (of species and functional groups) responded to current or previous year rainfall over the 15 year monitoring period, and these responses were greater than differences between reserves. This indicates that even large differences in reserve management do not override the effect on inter-annual rainfall on these semi-arid ecosys-

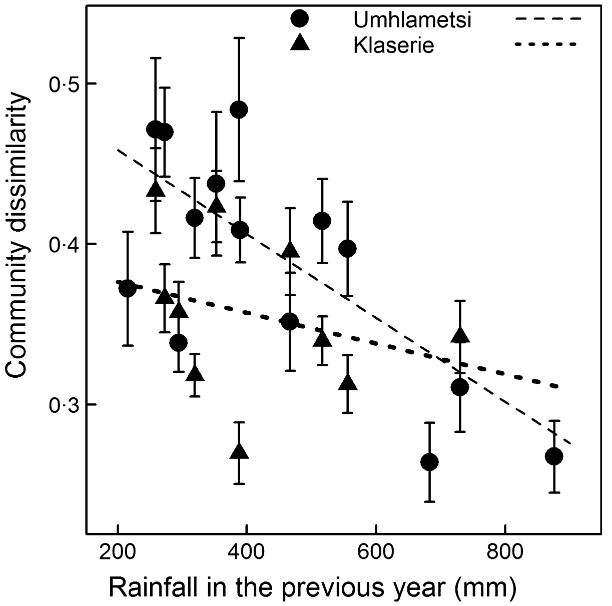

Fig. 4. Average compositional change (as measured by the Bray–Curtis dissimilarity index) over all the sites, vs. rainfall of the previous year, for each reserve. Error bars show one SE. Lines are predictions from the linear mixed-model.

tems. More of the variation in basal cover and community composition was associated with variation between years (time) than between all sites, regardless of reserve. This indicates that temporal variation in weather plays a far larger role than landscape-level spatial variation, even between very different management units.

Nonetheless significant differences between reserves of different size and with different management regimes were found. The smaller reserve, with higher waterhole density and a history of higher grazer densities, showed reduced responsiveness of vegetation structure to rainfall but higher species-level compositional change following low rainfall years. These differences are likely to be a result of differences in grazer density, which is known to have large effects on both the structure and the composition of herbaceous vegetation (Kelly & Walker 1976; Milchunas & Lauenroth 1993; Illius & O'Connor 1999).

BASAL COVER

The increase in tuft diameter with previous year rainfall and previous year tuft diameter indicates that tuft diameter was mainly determined by carried-over effects from the previous season rather than by current season conditions. As there is no storage of water in the soil between years in these semi-arid ecosystems, this lag effect is likely to be the result of storage of nutrients and/or carbohydrates in underground plant parts. Perennial grasses may increase resource allocation to roots late in the growing season during wet years (Snyman 2005, 2009) which would allow more above-ground growth at the onset of rain in the following wet season, resulting in larger tufts. While the larger reserve in this study had larger tufts, the carry-over effect of tuft diameter was evident in both reserves. Higher grazer density in the smaller reserve may have caused tufts to be smaller, however these smaller plants were still able to allocate resources to storage and subsequently increase their size following a high rainfall year. Thus it appears that intermittent wet years prevent a continuous decline, and eventual death, of perennial grasses in these systems.

Unlike tuft diameter, distance to tuft was determined by both the carried-over information from the previous year and by the current year's environmental conditions. Distance to tuft in the current year was positively related to tuft distance in the previous year but this effect was reduced, and eventually disappeared, with increasing rainfall. Therefore while sequential dry years result in a reduced response of tuft distance to rainfall, above average rainfall appeared to 'reset' the basal cover of these systems. The amount of rainfall at which the effect of previous year's distance to tuft on current year's distance to tuft disappeared was about 150 mm higher in the smaller reserve. Therefore, except in very high (> 750 mm) rainfall years, a lower basal cover is expected in this reserve compared to the larger one. Such interactive effects between rainfall and grazing on vegetation are well known in semi-arid savannas, where high herbivore densities combined with successive dry years cause high tuft mortality (O'Connor & Pickett 1992; O'Connor 1994; Fynn & O'Connor 2000).

Since tuft diameter did not increase with current season rainfall, the decrease of distance to tuft with current year rain could not have been simply a result of tufts getting larger. Rather, the density of tufts must have increased in wet years as predicted by O'Connor (1993). Greater seedling emergence in wet years (Dye & Walker 1987; O'Connor 1996; Veenendaal, Ernst & Modise 1996; Zimmermann *et al.* 2008) is likely to cause the decrease in distance to tuft by increasing tuft density. While the exact relationship between basal cover and 'distance to tuft' and 'tuft diameter' is not known for our study sites, it is axiomatic that a larger tuft size combined with a smaller inter-tuft distance indicates higher basal cover. Considering the individual responses of tuft diameter and tuft distance to previous and current year rainfall (Figs 1 and 2), basal cover must have increased during and following wet years. While direct effects of rainfall on basal cover are often inferred from studies comparing sites with different rainfall (Paruelo *et al.* 1999; Wiegand *et al.* 2004), the use of long-term data here reveals that rainfall effects are actually lagged. This is supported by a handful of other studies in semi-arid southern African savannas (Thrash 2000; Peel, Davies & Hurth 2004) and grasslands (Wiegand *et al.* 2004) and North-American savannas (Fuhlendorf, Briske & Smeins 2001) and grasslands (Gibbens & Beck 1988; Anderson & Inouye 2001).

COMMUNITY COMPOSITION

A loss of perennial grasses was expected for the smaller reserve. While absolute abundance was not measured, relative abundance of perennial grasses was similar between the reserves and increased with rainfall. Perennial grasses typically have higher leaf production than annual grasses and forbs, and the four most abundant perennial grasses in this study are regarded as good forage species (van Oudtshoorn 1999). Therefore even on the smaller reserve, higher rainfall years would have increased forage supply, and might play a more important role than on the larger reserve – both in terms of maintaining populations of grazers and in preventing the death of perennial grass plants. This requires further investigation, as the frequency of high rainfall years is likely to change with global climate change (IPCC 2007).

While the data did not allow for the analysis of changes in the absolute abundance of the dominant species, the dissimilarity results provide evidence that the relative abundance of the most common species changed significantly in response to annual rainfall, and with a much greater magnitude in the smaller reserve. It is possible that the lower cover of perennial grasses in the smaller reserve resulted in reduced competition with forbs and annual grasses, allowing different species of these groups to flourish – at least during dry years when perennial grasses did not show high relative abundance. Since the abundance of these less palatable species appear to be important determinants of both forage supply and plant diversity, more detailed studies of their dynamics are needed. Furthermore, the effect of rainfall was found to be lagged, which has not been reported for other African savannas or other semi-arid ecosystems.

MANAGEMENT IMPLICATIONS

Reserves such as the smaller one in this study are often perceived to be either degraded, or on the path to degradation, due to their relatively small and fenced area, high herbivore densities, and many waterholes. While we found slight differences in basal cover and community composition between this reserve and a much larger neighbouring reserve, there were no clear indications of any degradation to the herbaceous plant community. The lack of time trends in the analysed variables for vegetation structure and functional groups is particularly insightful, as this indicated a lack of evidence for any slow responses of the vegetation that might take decades or longer to manifest. The fact that the smaller reserve has maintained a higher density of grazers for over a decade supports this finding. It is of course possible that the effects of the management strategies on the smaller reserve have yet to manifest. However, the relatively stronger effects of rainfall over reserve suggest that high rainfall years simply override negative changes in the herbaceous layer resulting from management actions, and have prevented any serious degradation from developing. This overriding effect of rainfall could also explain why even in communal rangelands in the region (where stocking density is even greater than in the smaller reserve here), basal cover has been found to be higher than in neighbouring reserves and commercial cattle farms (Parsons, Shackleton & Scholes 1997). If the climate for the region were to remain as it has for the past two decades, we should conclude that smaller reserves (and their associated management strategies) are able to conserve ecosystem processes as well as larger ones.

The advent of global climate change makes such a conclusion tenuous. While predictions of statistically downscaled versions of some major global circulation models differ for the exact change in annual rainfall, there is general agreement that inter-annual variability will increase (Hewitson & Crane 2006; Lumsden, Schulze & Hewitson 2009). Therefore, these reserves are likely to experience even drier dry years and wetter wet years. It is probable that a year drier than the driest year in this study, or an interval between wet years longer than the longest interval here, would result in far more pronounced changes. This is primarily because perennial grasses will eventually die without adequate water supply, with large consequences for basal cover and herbaceous community composition, as well as forage supply. In the future the intermittent decline of basal cover, perennial grasses, and other changes in community composition evident in this study, may become permanent in the smaller reserve following a drought of unsurpassed intensity. A more useful conclusion is therefore that smaller reserves will be more vulnerable to the more extreme rainfall patterns that are likely as climate change progresses. To counter this, new management interventions, involving a reduction of herbivore densities, will be necessary. Reducing the number of waterholes is a simple means to achieve this, although this may be unpopular due to the importance of these waterholes to tourists and hunters. Alternatively, new strategies could be devised to manage grazer populations more dynamically, with stocking rates being reduced during key periods to allow herbaceous plants, and perennial grass in particular, time to regenerate. Further research is needed to establish whether it would be more effective to reduce stocking density during wet years or dry years. Long-term data series will be crucial to answer such research questions, as well as record the responses of ecosystems in smaller reserves to global climate change.

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References

Allen, R.B., Wilson, J.B. & Mason, C.R. (1995) Vegetation change following exclusion of grazing animals in depleted grassland, central Otago, New Zealand. *Journal of Vegetation Science*, **6**, 615–626.

Anderson, J.E. & Inouye, R.S. (2001) Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs*, **71**, 531–556.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Boone, R.B. & Hobbs, N.T. (2004) Lines around fragments: effects of fencing on large herbivores. *African Journal of Range and Forage Science*, **21**, 147–158.

Boone, R.B., BurnSilver, S.B., Thornton, P.K., Worden, J.S. & Galvin, K.A. (2005) Quantifying declines in livestock due to land subdivision. *Rangeland Ecology & Management*, **58**, 523–532.

Chape, S., Harrison, J., Spalding, M. & Lysenko, I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Royal Society Philosophical Transactions Biological Sciences*, **360**, 443–455.

Deshmukh, I.K. (1984) A common relationship between precipitation and grassland peak biomass for east and southern Africa. *African Journal of Ecology*, **22**, 181–186.

Dye, P.J. & Walker, B.H. (1987) Patterns of shoot growth in a semi-arid grassland in Zimbabwe. *Journal of Applied Ecology*, **24**, 633–644.

Foran, B.D., Tainton, N.M. & de Booysen, P.V. (1978) The development of a method for assessing veld condition in three grassveld types in Natal. *Proceedings of the Grassland Society of Southern Africa*, **13**, 27–33.

Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R.E., Haydon, D.T., Holt, R.D. & Abrams, P.A. (2005) Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*, **8**, 328–335.

Fuhlendorf, S.D., Briske, D.D. & Smeins, F.E. (2001) Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Applied Vegetation Science*, **4**, 177–188.

Fynn, R.W.S. & O'Connor, T.G. (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology*, **37**, 491–507.

Gibbens, R.P. & Beck, R.F. (1988) Changes in grass basal area and forb densities over a 64-year period on grassland types of the jornada experimental range. *Journal of Range Management*, **41**, 186–192.

Gibson, D.J. & Hulbert, L.C. (1987) Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio*, **72**, 175–185.

Hardy, M.B. & Tainton, N.M. (1993) Towards a technique for determining basal cover in tufted grasslands. *African Journal of Range and Forage Science*, **10**, 77–81.

Hewitson, B.C. & Crane, R.G. (2006) Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. *International Journal of Climatology*, **26**, 1315–1337.

Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813.

IPCC (2007) Climate change 2007: the physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor & H.L. Miller), pp. 847–890. Cambridge University Press, Cambridge.

Kelly, R.D. & Walker, B.H. (1976) The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia. *Journal of Ecology*, **64**, 553–576.

Knapp, A.K. & Smith, M.D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481–484.

Knoop, W.T. & Walker, B.H. (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, **73**, 235–253.

Lauenroth, W.K. & Sala, O.E. (1992) Long-term forage production of North-American shortgrass steppe. *Ecological Applications*, **2**, 397–403.

Le Houerou, H.N. (1984) Rain use efficiency – a unifying concept in arid-land ecology. *Journal of Arid Environments*, **7**, 213–247.

Ludwig, J.A., Tongway, D.J., Eager, R.W., Williams, R.J. & Cook, G.D. (1999) Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landscape Ecology*, **14**, 557–566.

Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J. & Imeson, A.C. (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology*, **86**, 288–297.

Lumsden, T.G., Schulze, R.E. & Hewitson, B.C. (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in southern Africa under conditions of climate change. *Water SA*, **35**, 649–656.

Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.

Newmark, W.D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the Environment*, **6**, 321–328.

O'Connor, T.G. (1985) *A Synthesis of Field Experiments Concerning the Grass Layer in The Savanna Regions of Southern Africa*. South African National Scientific Programmes report 114. Council for Scientific and Industrial Research, Pretoria.

O'Connor, T.G. (1993) The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. *Journal of Applied Ecology*, **30**, 119–132.

O'Connor, T.G. (1994) Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology*, **31**, 155–171.

O'Connor, T.G. (1996) Hierarchical control over seedling recruitment of the bunch-grass *Themeda triandra* in a semi-arid savanna. *Journal of Applied Ecology*, **33**, 1094–1106.

O'Connor, T.G., Haines, L.M. & Snyman, H.A. (2001) Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology*, **89**, 850–860.

O'Connor, T.G. & Pickett, G.A. (1992) The influence of grazing on seed production and seed banks of some African savanna grasslands. *Journal of Applied Ecology*, **29**, 247–260.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2009) *Vegan: Community Ecology Package*. The R Foundation for Statistical Computing, Vienna, Austria.

van Oudtshoorn, F. (1999) *Guide to Grasses of Southern Africa*. Briza Publications, Pretoria.

Owen-Smith, R.N. (2004) Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, **19**, 761–771.

Parsons, D.A.B., Shackleton, C.M. & Scholes, R.J. (1997) Changes in herbaceous layer condition under contrasting land use systems in the semi-arid lowveld, South Africa. *Journal of Arid Environments*, **37**, 319–329.

Paruelo, J.M., Lauenroth, W.K., Burke, I.C. & Sala, O.E. (1999) Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems*, **2**, 64–68.

Peel, M.J.S., Davies, R. & Hurth, R. (2004) The value and costs of wildlife and wildlife-based activities in the eastern Lowveld savanna. *Woodlands in South Africa – Policy, People and Practice* (eds M.J. Lawes, H.A.C. Eeley, C.M. Shackleton & B.G.S. Geach), pp. 775–795. University of KwaZulu-Natal Press, Durban.

Peel, M.J.S., Kruger, J.M. & MacFadyen, S. (2007) Woody vegetation of a mosaic of protected areas adjacent to the Kruger National Park, South Africa. *Journal of Vegetation Science*, **18**, 807–814.

Peel, M.J.S., Kruger, J.M. & Zacharias, P.J.K. (2005) Environmental and management determinants of vegetation state on protected areas in the eastern Lowveld of South Africa. *African Journal of Ecology*, **43**, 352–361.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2009) *nlme: Linear and Nonlinear Mixed Effects Models*, The R Foundation for Statistical Computing, Vienna, Austria.

Quinn, G.P. & Keough, M.J. (2003) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.

R Development Core Team (2009) *R 2.9.0*. The R Foundation for Statistical Computing, Vienna, Austria.

Rutherford, M.C. (1980) Annual plant-production precipitation relations in arid and semi-arid regions. *South African Journal of Science*, **76**, 53–56.

Searle, K.R., Hobbs, N.T. & Jaronski, S.R. (2010) Asynchrony, fragmentation, and scale determine benefits of landscape heterogeneity to mobile herbivores. *Oecologia*, **163**, 815–824.

Snyman, H.A. (1998) Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. *Journal of Arid Environments*, **39**, 645–666.

Snyman, H.A. (2004) Short-term response in productivity following an unplanned fire in a semi-arid rangeland of South Africa. *Journal of Arid Environments*, **56**, 465–485.

Snyman, H.A. (2005) Rangeland degradation in a semi-arid South Africa – I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. *Journal of Arid Environments*, **60**, 457–481.

Snyman, H.A. (2009) Root studies on grass species in a semi-arid South Africa along a degradation gradient. *Agriculture Ecosystems & Environment*, **130**, 100–108.

Snyman, H.A. & du Preez, C.C. (2005) Rangeland degradation in a semi-arid South Africa – II: influence on soil quality. *Journal of Arid Environments*, **60**, 483–507.

Swemmer, A.M., Knapp, A.K. & Snyman, H.A. (2007) Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology*, **95**, 780–788.

Tainton, N.M. (1999) *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg.

Thrash, I. (2000) Determinants of the extent of indigenous large herbivore impact on herbaceous vegetation at watering points in the north-eastern lowveld, South Africa. *Journal of Arid Environments*, **44**, 61–72.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843–845.

Veenendaal, E.M., Ernst, W.H.O. & Modise, G.S. (1996) Effect of seasonal rainfall pattern on seedling emergence and establishment of grasses in a savanna in south-eastern Botswana. *Journal of Arid Environments*, **32**, 305–317.

Venter, F.J. (1986) Soil patterns associated with the major geological units of the Kruger National Park. *Koedoe*, **29**, 14.

Wiegand, T., Snyman, H.A., Kellner, K. & Paruelo, J.M. (2004) Do grasslands have a memory: modeling phytomass production of a semiarid South African grassland. *Ecosystems*, **7**, 243–258.

Witkowski, E.T.F. (1983) *Ecology of the Klaserie Private Nature Reserve*. MSc thesis, University of the Witwatersrand.

Witkowski, E.T.F. & O'Connor, T.G. (1996) Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Vegetatio*, **124**, 9–23.

Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J., Munkemuller, T. & Linstadter, A. (2008) Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *Journal of Ecology*, **96**, 1033–1044.

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Supporting Information

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

Appendix S1. Number of monitored sites for each reserve and rainfall per growing season.

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