THE INFLUENCE OF FIRE-GRAZER INTERACTIONS ON FORB COMMUNITIES IN A HIGHVELD GRASSLAND

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Table of Contents

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ABSTRACT

In southern Africa, disturbance contributes to the heterogeneity of grassland and savanna ecosystems. Fire and grazing act as the primary disturbances in these systems, and interactions between the two are common. As such, an understanding of the relationship between fire and grazing is essential for the conservation of biotic diversity and the production of high-quality forage for game and livestock. Frequent fires followed by concentrated grazing have been shown to facilitate patches of short, palatable grasses ("grazing lawns") within grassland and savanna landscapes. The effects of grazing lawn management on other aspects of biodiversity have received little attention. Forbs (non-graminoid, herbaceous plants) are an important component of grassland ecosystems, but how they respond to disturbance is largely unknown. This study compared changes in forb communities on and off of firebreaks (an extreme example of a grazing lawn) in a high altitude mesic grassland. Native herbivore biomass was significantly higher on firebreaks than in the surrounding lightly grazed matrix and the firebreaks, while more compacted, did not show significant signs of degradation. There were no significant differences in forb abundance or richness between annually burned and intermittently burned plots, and there was no species turnover associated with the annually burned, heavily grazed treatment. Species-specific differences in functional traits on annually burned and intermittently burned plots were likely a function of light limitation, as mammalian palatability scores were nominal. Ultimately, ten years of intensive fire and grazing have had minimal impact on forb communities in a high altitude mesic grassland. The results indicate that in this type of Highveld grassland, heavily grazed and annually burned patches are not detrimental to the forb community and clearly enhance habitat diversity for grazers.

Keywords: grazing lawn, fire-grazer interactions, forb, grassland, biodiversity

1. Introduction

1.1 Fire and grazing as disturbances in grassland systems

Disturbance plays a critical role in shaping the heterogeneity of grassland and savanna systems. The primary disturbances in natural grasslands are fire and herbivory, which act as top-down, abiotic and biotic consumers that dictate the structure of vegetative communities (Tainton & Mentis 1984; Noy-Meir 1995; Collins et al. 1998; Bond & Keely 2005). In conjunction with climatic variables, fire and herbivory modify ecosystem processes and determine patterns of plant diversity (Langevelde et al. 2003; Bond 2005; Burkepile et al. 2016). Fire is an abiotic consumer that directly influences plant communities by removing herbaceous biomass, increasing primary productivity, and limiting woody plant recruitment (Bond & Keeley 2005; Bowman et al. 2016). As biotic consumers, grazers remove herbaceous biomass, and continued grazing excludes fire by keeping grass biomass low (Norton-Griffiths 1979; Waldram et al. 2008). The relative importance of fire and herbivory vary from region to region, and one driver tends to dominate at a particular site (Archibald & Hempson 2016). Different scenarios promote the dominance of fire versus grazing, namely continuity in space versus continuity in time (i.e. fires need continuous fuel beds while herbivores need a constant supply of forage) (Archibald & Hempson 2016).

Fire and grazing are primarily viewed as interactive, rather than separate disturbance mechanisms (Noy-Meir 1995; Bond 2005; Fuhlendorf et al. 2005). In grassland and savanna systems, fire can alter the way that herbivores use the landscape, which in turn impacts plant diversity (Van Wilgen & Scholes 1997; Burkepile et al. 2016; Collins 2006). For example, animals are attracted by the green flush of vegetation that occurs immediately after a fire. Post-burn vegetation following a large fire can cover the landscape and effectively disperse grazers

(McNaughton et al. 1988), whereas small fires concentrate grazers on burned patches (Burkepile et al. 2016). A recent study by Burkepile et al. (2016) indicates that small fire treatments can continue to attract herbivores after more than 50 years of annual/biennial burns. Experimental work in the semi-arid savannas of Kruger National Park, South Africa has even shown that concentrated grazing can switch the dominant consumer from fire to herbivores (Donaldson et al. in review).

Continuous, concentrated grazing can create a lawn-like state (i.e. grazing lawn), characterized by prostrate, short ecotypes with small leaves (McNaughton 1984). In some cases, these lawns are part of a positive feedback of heavy herbivory and palatable, productive grass species; in other cases, grazing lawns are heavily degraded with high levels of soil compaction and unpalatable vegetation (Augustine & McNaughton 1998; Hempson et al. 2015). Grazing lawns have the potential to contribute to the biodiversity and productivity of grassland systems, but elucidation of the two different trajectories is required to understand the implications of their management.

1.2 Impacts of grazing on grassland communities

At low grazing intensities, canopy removal leads to a rise in the diversity of less vertical species but as grazing intensity increases, diversity rapidly decreases (Milchunas et al 1988). Milchunas et al. (1988) also suggested that this general pattern is likely to be mediated by the “evolutionary history” of grazing at a site, as sites with a long grazing history would have had time to develop a grazer-adapted flora. In the context of Africa, this implies that “rich savannas” (arid, nutrient rich) and “poor savannas” (mesic, nutrient poor) may respond differently to shifting herbivore regimes, in part because of their different evolutionary histories (Milchunas et al. 1988). While indigenous grazers such as eland and wildebeest have always been present in mesic systems, the combination of relatively high productivity (>700 mm rainfall) but poor winter forage (high C:N ratios) means that most of the above-ground biomass was probably consumed by fire each year (Archibald & Hempson 2016). These grasslands have the potential to be significantly altered by switching from fire to herbivory as the dominant consumer, as the plant community is characterized by fire-prone species that are poor competitors in the face of defoliation.

Shifting herbivore regimes as a result of human activity present unique questions regarding the response of plant communities, particularly in mesic systems. Informed management of modified disturbance regimes is important for the provision of ecosystem services and the maintenance of biotic diversity. Studies of grazing lawns have had a predominant focus on grass community composition, and this is particularly true of studies of wildlife on grazing lawns (McNaughton 1984; Verweij et al. 2006; Burkepile et al. 2016). However, in grassland and savanna communities, grass species diversity is a very small part of overall species diversity (Uys 2006; Van Coller et al. 2013). The heavy agronomic focus of grazing studies means other herbaceous species have been largely ignored (but see Scott-Shaw et al. 2014; Siebert and Scogings 2015). The scope of grazing lawn evaluations must expand beyond grass species to other aspects of plant diversity, particularly in mesic systems where a short evolutionary history of grazing may confound the switch between disturbance types.

1.3 Forbs on grazing lawns

Forbs are an important yet understudied component of grassland diversity. They compose most of the species richness in grasslands (Uys 2006; Van Coller et al. 2013) and are an important food source for wildlife and cattle (Owen-Myers 1989; Siebert & Scogings 2015). The ecological consequences of their removal are largely unknown, as is their functional role in the system. A few studies of grassland or savanna forbs have examined their response to wildlife grazing (see Little et al. 2015, Scott-Shaw & Morris 2015, Siebert & Scogings 2015), though none have considered forbs in the context of small patch burns. Often, increases in forb cover are considered a sign of grassland degradation (Hayes & Holl 2003), and in general their contributions to carbon cycling, secondary productivity, and biodiversity have been under-recognized: a recent study shows that even in sites characterized as 100% C4 grassland cover, 30% of the belowground carbon is contributed by C3 plants, presumably forbs (Angelo & Pau 2015).

Patterns of forb diversity and wildlife utilization on and off of grazing lawns can offer a nuanced view of the conditions facilitating grassland degradation, and will be useful for informing managers of the broader implications of grazing regimes for biodiversity. Annual burning combined with heavy grazing has the potential for one of two trajectories: a) to facilitate forb diversity and abundance by reducing competition with tall grass species for light (McNaughton 1984), or b) to limit forb diversity through herbivory and reduced soil moisture.

1.4 Trait-based approach

Studies of vegetation dynamics and disturbance are moving from species-centered to trait-based approaches, as the latter are appropriate for identifying ecosystem processes (Kattge et al. 2011). Forb communities have been shown to exhibit functional responses to grazing regimes, suggesting that functional traits could be useful for describing these communities and understanding ecological processes across environmental gradients (Cingolani et al. 2005). Studies of cattle grazing in other systems have identified forb traits that respond to herbivory, specifically life span and colonization ability (Hayes & Holl 2003; Bullock et al. 2001).

Identifying forb functional responses to annual burns and concentrated grazing has the potential to contribute to regional and global knowledge of grazing responses and inform models of future change. Plant traits are clearly linked to regional disturbance regimes. For example, a global synthesis of plant trait responses to grazing indicates a mostly neutral response of forb communities in arid regions (Diaz et al. 2007), while a regional studies suggests a positive feedback between herbivory and palatable forb species (Siebert & Scogings 2015). Selective grazing could be a mechanism to explain any functional diversity that exists on grazing lawns (Bullock et al. 2001). Localized trait-based studies can help us to understand the implications of grazing for the functionality of forb communities and vice versa.

1.5 Aims and objectives

The primary aims of this study are to 1) assess whether forbs are more abundant on annually burned and heavily grazed sites, 2) determine how floral diversity is represented on grazing lawns (in terms of species composition and functional traits), and (3) investigate the consequences of this floral diversity for herbivores. Highveld grassland management relies heavily on fire, and other studies in this area have identified a unique, fire-adapted flora (e.g. Uys 2004). Thus, this study will identify changes in floral diversity associated with frequent fire and heavy grazing. Although the heavily grazed areas are also more frequently burned than the surrounding grassland, we make the assumption that any response we see is largely a grazing response. There are no fire-only or grazing-only treatments, and this study does not have the capacity to separate the effects of fire and grazing.

This study will address the following hypotheses: 1) forb abundance and species richness are greater on annually burned and heavily grazed sites, as stocking rates are low enough that defoliation will facilitate the diversity of more vertical species (Milchunas et al. 1988); 2) frequent fire and heavy grazing initiate a turnover in forb communities, such that a unique graze-adapted flora is associated with these areas; and 3) forb species have a different suite of functional traits on annually burned, heavily grazed sites, with a specific graze-adapted flora on grazing lawns.

2. METHODS

2.1 Study Site

Kromdraai Valley Reserve (25°58'40"S, 27°46'43"E), is a 1200 ha conservancy northwest of Johannesburg, South Africa (Figure 1). The conservancy is situated within the Cradle of Humankind, an area of Highveld grassland characterized by rolling hills and rocky outcrops, underlain by dolomitic bedrock (Hilton-Barber & Berger 2004). The soils are nutrient poor and sandy, with a low clay content (Elof 2010). The Highveld region experiences summer rains, and the average rainfall at the conservancy is approximately 700 mm per annum (Kromdraai Valley Reserve, unpublished data). The study area falls within the Carletonville Dolomite Grassland, and consists of mainly grasses and forbs, with a few trees scattered throughout the landscape (Mucina et al. 2005). Poaceae, Asteraceae, and Fabaceae are the dominant families within this grassland type (Siebert and Siebert 2005). Common grass species at the study site include *Aristida spp., Brachiaria serrata, Setaria spp., Cymbopogon caesius, Eragrostis spp.,* and *Themeda triandra* (F. Skhosana, unpublished data). Common forb species include *Acalypha angustata, Hermannia depressa, Felicia muricata,* and *Helichrysum rugulosum*. The wild herbivore population is approximately 256 individuals (Kromdraai Valley Reserve, unpublished data). Dominant species include Impala, Kudu and the grassland specialists Blue Wildebeest, Zebra, Red Hartebeest, and Waterbuck (Table 1).

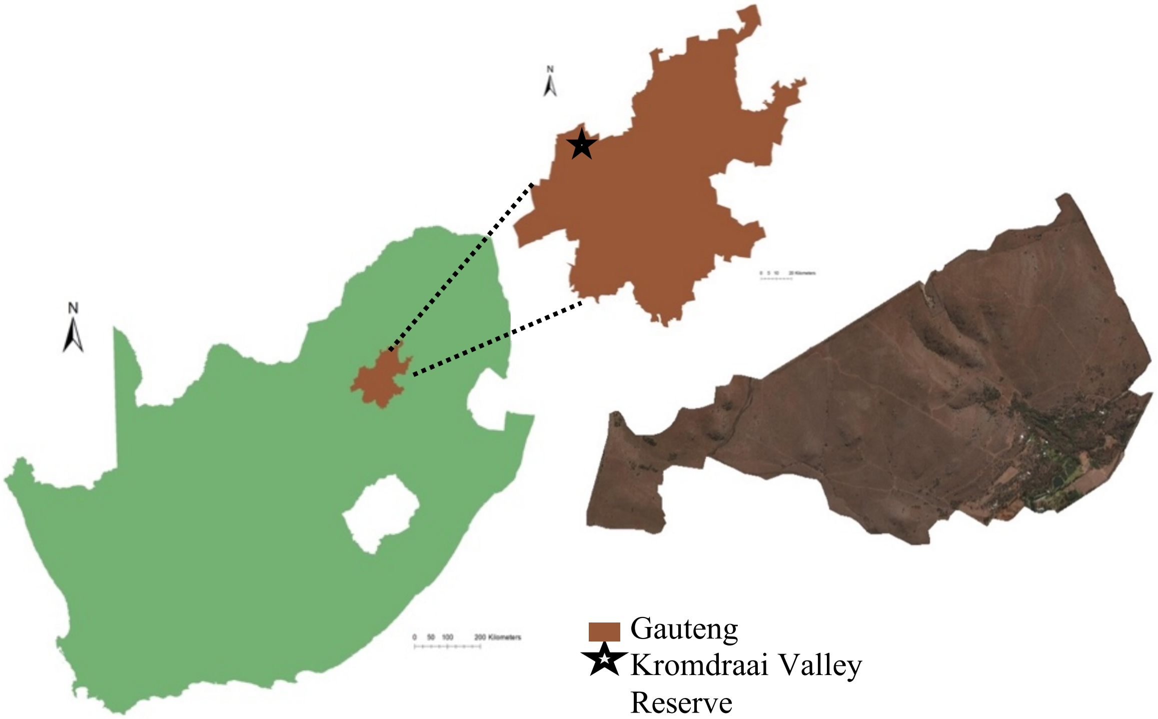

Figure 1 Kromdraai Valley Reserve study site, located in western Gauteng, South Africa.

Table 1 Kromdraai Valley Reserve wild herbivore abundances and feeding strategies.

Species	**Count**	**Type of feeder**
Impala (*Aepyceros melampus*)	42	Mixed
Blue Wildebeest (*Connochaetes taurinus*)	35	Grazer
Zebra (*Equus quagga*)	25	Grazer
Kudu (*Tragelaphus strepsiceros*)	25	Browser
Red Hartebeest (*Acelaphus buselaphus*)	25	Grazer
Waterbuck (*Kobus ellipsiprymnus*),	24	Grazer
Blesbok (*Damaliscus pygargus*)	22	Grazer
Warthog (*Phacochoerus africanus*)	20	Mixed
Bushbuck (*Tragelaphus scriptus*)	15	Mixed
Grey Duiker (*Sylvicapra grimmia*)	10	Mixed
Mountain Rhebuck (*Pelea capreolus*)	7	Mixed
Gemsbok (*Oryx gazella*)	3	Grazer
Giraffe (*Giraffa camelopardalis*)	3	Browser

This project is part of a larger experimental study assessing the use of small burns to manipulate fire-grazer interactions. Firebreaks represent an extreme example of small, frequent burns, and some firebreaks at the conservancy had been burned annually for the past 10 years (Figure 2). The adjacent tall-grass matrix had historically lower levels of both fire and grazing – fires occur here at approximately 3 year return periods, and the indigenous grazer biomass grazes this matrix lightly, with concentrated grazing patches under the trees, on the firebreaks, and in the valley (Archibald & Bond 2003). Stocking rates are low compared with commercial reserves, with a current stocking rate of 20.8 hectares per large animal unit (ha LAU^{-1}) (Kromdraai Valley Reserve, unpublished data) where one LAU^{-1} equates to the metabolic requirements of one 454 kg cow (Tainton 1999). In high altitude grasslands, a carrying capacity of 3 to 5 ha LAU^{-1} is advised (Tainton 1999). Nevertheless, this herbivore density is still representative of what would be expected for a wildlife population on these soils (~ 3400 kg/km^2, Fritz & Duncan 1994), with a total grazer biomass of 2179 kg/km^2, total browser biomass of 501 kg/km^2, and total mixed feeder biomass of 223 kg/km^2 (F. Skhosana, unpublished data).

A previous study had explored changes in grass community composition and ecosystem function on and off of the firebreaks, providing a baseline for this study of ecosystem function as it relates to forb community composition (F. Skhosana, unpublished data).

Figure 2 An example of an intermittently burned tall-grass matrix (left) and the adjacent annually burned firebreak (right) at Kromdraai Valley Reserve.

2.2 Sampling design

A total of eleven paired plots on four firebreaks of similar sizes were sampled. Firebreaks with similar soil type and geology were identified, and two to three paired plots within each firebreak (referred to as A, B, C, or D in Figure 3) were randomly selected. Plots were spaced at least 150 m apart along each fire break, at least 5 m inward from the edge of the firebreak. Intermittently burned 'control' plots were adjacent to the annually burned plots and at least 5 m inward from the edge of the tall-grass matrix. Non-grassy herbaceous vegetation was sampled in 1 m^2 plots, following the Modified-Whittaker design (Stohlgren et al. 1995). The 10 m^2 and the 100 m^2 plots were excluded, as it was not possible to sample them during the study period. 50 m transects were arranged parallel to the environmental gradient (transects run along the middle of each plot), and a 0.5 x 2 m (1 m^2) quadrat was placed at every 5 m along the transect (Figure 4). Counts of each species in the 1 m^2 subplot were recorded. In total, 10 x 1 m^2 subplots were sampled on each transect. The 10 subplots were pooled (i.e. all analyses represent count and species richness per site), so that the sampling scale of the plant data matched that of the environmental data: this was necessary for the ordinations. Each subplot was sampled twice, first in October (before the spring rains) and again in December (mid-way through the growing season). The October sampling was necessary to record the abundance and richness of ephemeral geophytes, which were only detectable early in the growing season. To avoid counting the same individual across seasons, the maximum frequency of each species per subplot was used in the analyses (Hickman & Hartnett 2002).

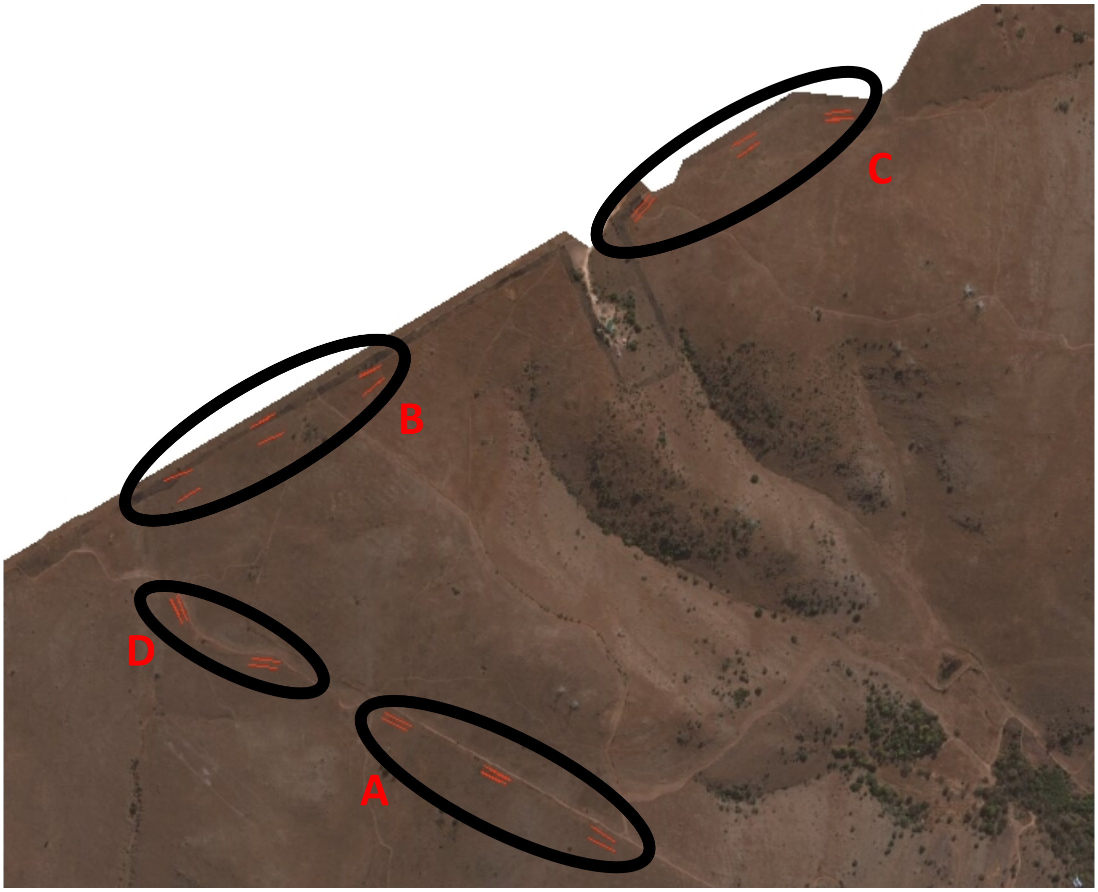

Figure 3 The four firebreaks (A, B, C, and D) and 11 paired sample sites (red lines) sampled at the Kromdraai Valley Farm conservancy.

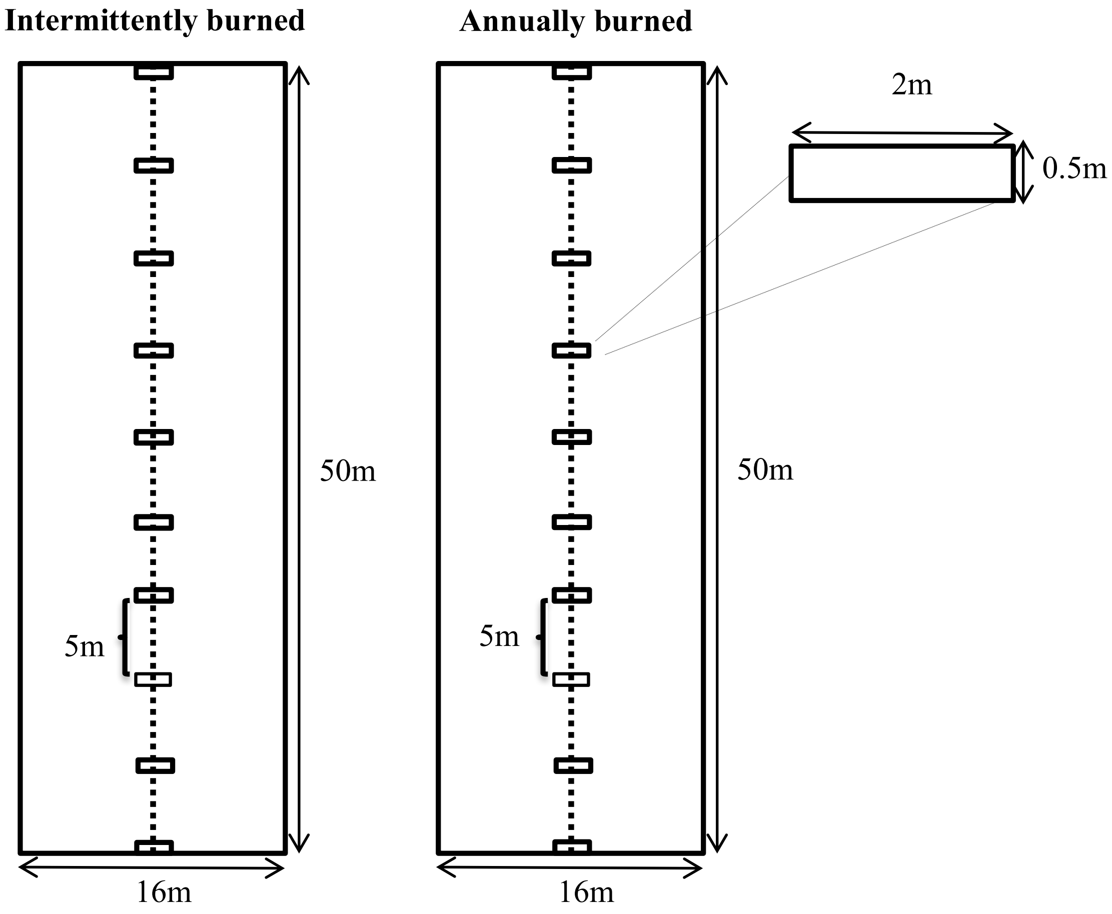

Figure 4 Forb sampling design, based on the Modified-Whittaker design.

2.3 Environmental and grazing variables

Elevation was recorded at the beginning and end of each transect (using a handheld Garmin eTrex 10), and the values were used to calculate percent slope and average elevation for each transect. Aspect was also recorded for each plot.

A soil penetrometer was used to measure soil compaction at the center of each transect and the fifth drop was reported. To ensure comparable measurements between plots, compaction was only measured during the December sampling. To obtain estimates of grass biomass, a disc pasture meter (Bransby & Tainton 1977) was dropped every five meters along each 50 m transect and an average was obtained from the ten height measurements. Average disc height was converted to grass biomass (kg ha^{-1}) using a linear calibration for moist highland grasslands, where $y = 358.7x – 746.4$ (Little *et al.* 2015). Little et al. (2015) obtained an R^2 value of 0.91 for their calibration which was higher than previous calibrations (compare with Bransby & Tainton 1977). Percent bare ground was visually estimated in each 1 m^2 subplot, and then the values from the 10 subplots were averaged to get an estimate for each 10 m^2 plot. Grass biomass and percent bare ground was measured in October and again in December, though only the December measurements were used in the analyses.

To measure soil moisture and qualify soil texture, a 5 x 5 x 10 cm^3 soil core was taken from the beginning and end of each 50 m transect, and the two samples were mixed together. Soil moisture was measured in October and December, though only the October measurements were used in the analysis, as there was a malfunction with drying oven. While soil moisture values from December would have been more robust (i.e. along with the December estimates of compaction, percent bare ground, and grass biomass), other soil moisture data from the site showed the same trends as the October measurements (F. Skhosana, unpublished data). Because the environmental data were not statistically normal (Shapiro Wilks test), non-parametric Kruskal-Wallis tests were used to compare soil compaction, grass biomass, bare ground, and soil moisture on and off of the firebreaks.

Grazer visitation rates on and off of the firebreaks and the grazer selectivity index were based on an honours project by Alekzandra Szewczuk. Data were collected from camera traps set up between January and May 2016, when grass biomass was at a maximum. Grazer densities (kg/km^2) were used for the selectivity index to account for the fact that the cameras sometimes sampled slightly different areas of the firebreaks and tall grass matrix. Grazer selectivity was quantified as the grazer biomass (kg)/km^2 on the firebreak / (grazer biomass (kg)/km^2 on the firebreak + grazer biomass (kg)/km^2 in the tall-grass matrix). A value >0.5 indicates grazer preference for the firebreak. (see Sensenig et al. 2010 for a description of this metric). A non-paired Wilcoxon signed rank test was used to assess differences in selectivity on the two treatments.

2.4 Community composition

The guide by Van Wyk & Malan (1997) was used to identify all forbs and dwarf shrubs within each 1 m^2 subplot. As forbs were sparsely distributed, count was a more useful metric than percent cover. A sample of each species was brought back to the University of Witwatersrand herbarium to confirm the identification with the herbarium curators. Species names were verified/updated in consult with the Plants of Southern Africa annotated checklist (South African National Biodiversity Institute 2016). Signs of herbivory were recorded for each plant that was encountered and mammalian and invertebrate herbivory were differentiated between when possible (C. Parr, personal communication). An herbivory score (i.e. probability of being bitten) was computed for each of the dominant species and this score was used as a species-level functional trait in the multivariate analyses.

To compare forb species richness on and off of the firebreak, the Shapiro-Wilk method was used to test for normality, and a Welch's two-sample t-test was applied to the data. Diversity metrics were calculated for the two treatments, using the 'diversity' function in the 'vegan' package in R version 3.3.1 (Oksanen et al. 2013; R Core Team 2016) and Hill's numbers: H_0

(number of species), H_1 (exponential of Shannon's diversity index), and H_2 (inverse of Simpson's diversity index), as well as as a measure of Pielou's evenness (J) (Hill 1973).

The 'lmer' function in the 'lme4' package was used in R (Bolker et al. 2009; Bates et al. 2011; R Core Team 2016) to fit linear mixed models to diversity indices (i.e. H_0, H_1, H_2 and J). All models included treatment as a fixed effect and replicate (i.e. firebreak A, B, C, or D) as a random effect. Tukey's post-hoc tests with the Holm correction factor, using the 'ghlt' function in the 'multicomp' package (Hothorn et al. 2008; R Core Team 2016), were used to test for significant differences between treatments.

The 'indval' function in the 'labdsv' package in R (Dufrêne and Legendre 1997; Roberts 2013; R Core Team 2016) was used to calculate indicator values (IndVal), as a way of assessing species specificity and fidelity to a site. Specificity describes the species that are abundant in a specific habitat (relative abundance), while fidelity describes species that are primarily found in that habitat (relative frequency of occurrence): *IndVal = Specificity * Fidelity * 100* (Dufrêne and Legendre 1997). Good indicator species (ones with a high IndVal) can be used to give ecological meaning to groups of sites and classify sites by species characteristics rather than observed environmental variables.

The 'adonis' function in the 'vegan' package in R (Anderson 2001; McArdle and Anderson 2001; Oksanen et al. 2013; R Core Team 2016) was used to assess turnover in species composition between treatments. Adonis relates species turnover to environmental variables by computing a permutational manova (formerly "nonparametric manova") for the species data. The analysis partitions sums of squares for a multivariate data set, representing a robust alternative to a parametric MANOVA (Anderson 2001; McArdle and Anderson 2001). Environmental variables used in the analysis included treatment, slope, elevation, and aspect. Replicate (i.e. firebreak A, B, C, or D) was included as a random factor in the analysis.

2.5 Functional traits

Functional trait data at a species level was required in order to address the hypotheses and to provide an indication of how functional traits alter within a species in response to intensive fire and grazing (phenotypic response). Species-specific data was collected on the height and lateral spread of ten mature individuals of the most abundant forb species at the site, irrespective of whether they were located on or off the firebreak. 33 species made up 80% of total forb abundance at the site, and the analyses used these 33 species (see Appendix) to avoid giving too much weight to rare species (Pakeman & Quested 2007). To address the question of phenotypic response, the height and lateral spread of the six most abundant forb species (*Acalypha angustata, Hermannia depressa, Felicia muricata, Senecio venosus, Scabiosa columbaria,* and *Helichrysum rugulosum*) were recorded on and off of the firebreaks, following the trait measurement guidelines put forth in Cornillessen et al. (2003). 25 mature, uneaten individuals were selected on an annually burned plot and 25 were selected on the corresponding intermittently burned plot.

Individuals were sampled by walking downslope along the transect and measuring the first 25 (or ten) plants that were encountered. If two individuals were less than a meter apart, trait data was recorded for the first plant and the second plant was bypassed. All trait measurements were taken during the December sampling, when plant biomass was greatest (Cornillessen et al. 2003).

The Shapiro-Wilk method was used to test for normality and Welch's two-sample t-tests were used to compare the height and lateral spread of *Acalypha angustata, Hermannia depressa, Felicia muricata, Senecio venosus, Scabiosa columbaria,* and *Helichrysum rugulosum* on and off of the firebreaks. For the species-specific data, an average ratio of height to lateral spread was calculated for 25 individuals. The predictive power of the model was slightly better when using height and lateral spread, compared to the ratio of height to lateral spread, so both measurements were used in the multivariate analyses. Of the 33 species that composed 80% of total forb abundance, the least abundant species had 18 individuals. Therefore, the first 18 observations for each species were used to compute a standardized palatability score.

2.6 Trait—environment relationship

To investigate the relationship between forb traits and environment, RLQ and fourth-corner analyses were conducted using the 'ade4' package in R (Dray and Dufour 2007; R Core Team 2016). RLQ uses a co-inertia analysis to produce a single ordination of the three data tables, R (site x environment), L (species x site), and Q (species x trait) (Dray et al. 2003), whereas the fourth-corner approach combines the R, L, and Q tables into a fourth matrix that describes the trait-environment relationships (Legendre et al. 1997). While the two methods address similar ecological questions, the underlying approaches are different. Ideally, the fourth-corner and RLQ analyses should be combined to maximize the knowledge gained (Dray et al. 2014).

Prior to the RLQ analysis, a Hellinger transformation was performed on the species table to reduce the effect of abundant species (Legendre & Gallagher, 2001). The species table included 33 species, which composed 80% of the forb abundance on annually burned and intermittently burned plots (Pakeman & Quested 2007). Separate ordinations were performed on each table. First, the 'dudi.coa' function was used to apply a Correspondence Analysis (CA) to the species table (Dray & Dufour, 2007). All of the factors were assigned ordinal values (for example, the variable aspect was transformed into a variable SouthYES, SouthNO and included in the CA), as CA cannot use factors as variables. Species and site weights from this analysis were then used in the analysis of species traits and environmental variables. The environment table contained four variables: treatment (annually burned or intermittently burned), percent slope, elevation, and aspect (Table 2). The trait table contained five variables; probability of invertebrate herbivory, probability of mammalian herbivory, height, lateral spread, and perennial habit (versus annual). None of the environment or trait variables were strongly correlated (‘cor’ function in the ‘stats’ package in R).

Table 2 Environmental variables included in the Principle Coordinate Analysis.

Environmental variable	Unit of measurement
Elevation	Meters
Aspect	SouthYES = 1, SouthNO = 0
Slope	Percent
Treatment	Annually burned = 1, Intermittently burned = 0

Table 3 Trait variable included in the Correspondence Analysis.

Trait variable	Unit of measurement
Invertebrate palatability	Number bitten / 18
Mammalian palatability	Number bitten / 18
Height	Tallest point of vegetative growth (cm)
Lateral spread	Diameter at widest point (cm)
Perennial habit	PerennialYES = 1, PerennialNO = 0

As the environment and trait data were both mixes of qualitative and quantitative data, the 'dudi.hillsmith' function was used to perform Hill-Smith Principal Component Analyses (PCA) on each of these tables (Dray & Dufour 2007). The '*rlq'* function then combined the three separate analyses to maximize the covariance between the trait and environment scores, as mediated by the species abundances (Dray & Dufour, 2007).

To perform the fourth corner analysis, 49,999 permutations were applied to test the significance of associations between traits and environmental variables, with the permutation method set to model 1 (‘fourthcorner’ function). Model 1 permutes the abundance values for each species independently within each column of L (Legendre *et al.* 1997). The False Discovery Rate (fdr) method was used to correct for multiple testing (Benjamini & Hochburg 1995).

3. RESULTS

3.1 Environmental and grazing variables

Soil compaction was significantly higher on annually burned sites, with a mean penetration index (low penetration index equates to high soil compaction) of 44.3 mm/five blows, compared to 68.8 mm/five blows on intermittently burned sites (Figure 5; $\chi^2 = 5.83$, $p = 0.016$). There was no significant difference in bare ground or soil moisture between annually burned and intermittently burned sites ($\chi^2 = 3.38$, $p = 0.066$; $\chi^2 = 2.80$, $p = 0.094$). Standing grass biomass was significantly lower on annually burned sites, with a mean biomass of 341 kg ha^{-1}, compared to 2031 kg ha^{-1} on intermittently burned sites ($\chi^2 = 15.8$, $p = 7.039e^{-05}$) – however, standing grass biomass is not a reasonable indication of above-ground productivity in systems which are grazed (McNaughton 1979; Knapp et al. 2012) .

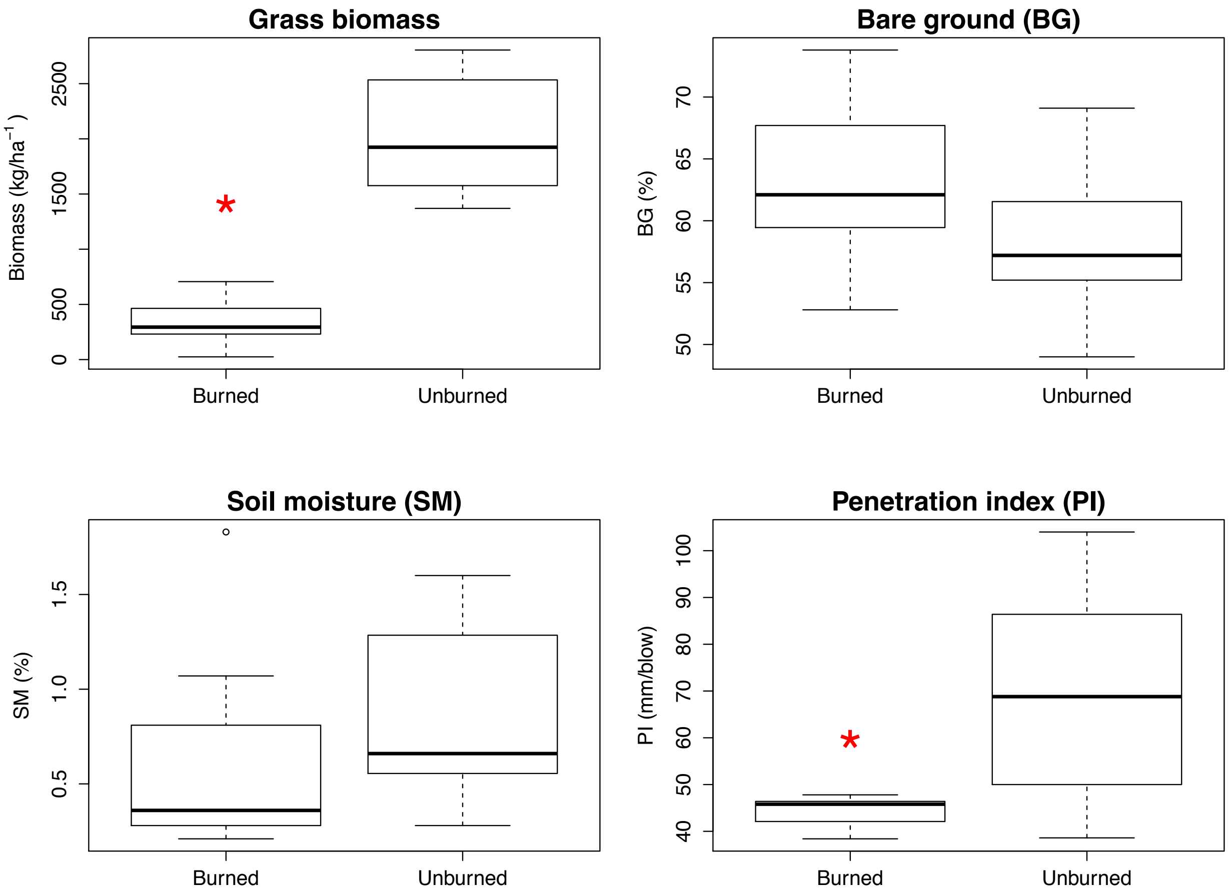

Figure 5 Mean grass biomass, percent bare ground, soil moisture, and soil compaction on annually burned (‘burned’) and intermittently burned (‘unburned’) sites. A red star indicates significant differences in the chi-square value of annually burned and intermittently burned plots.

The annually burned sites experienced a greater number of total grazer visitations than the intermittently burned sites ($N_{\text{Annually burned}} = 316$, $N_{\text{Intermittently burned}} = 160$; $p = 0.01563$). All six dominant herbivore species showed a strong preference for annually burned areas, as indicated by the grazer selectivity index calculated from grazer biomass per km^2 (Table 2). This included the mixed feeder impala and the tall-grass specialist Zebra – although these two species had lower preference scores (0.703 and 0.815, respectively) compared with over 0.9 for short grass specialists Wildebeest and Hartebeest.

Table 4 Grazer counts and grazer biomass per km^2 on annually burned and intermittently burned sites at Kromdraai Valley Reserve, obtained from camera trap data over a four-month period (January to May 2016). A selectivity index > 0.5 indicates preference for firebreak.

	Count		**Kg per km^2**		
	Annually burned	**Intermittently burned**	**Annually burned**	**Intermittently burned**	**Selectivity index**
Hartebeest	55	2	12.823	0.447	0.968
Blesbok	36	11	2.807	0.916	0.783
Impala	28	13	1.311	0.460	0.703
Wildebeest	17	2	4.299	0.789	0.903
Zebra	178	131	46.605	36.017	0.815
Gemsbok	2	1	0.656	0.174	0.687
Total	316	160	68.501	38.802	0.685

3.2 Community composition

In total, 3623 plants of 105 species were recorded within the 22 plots (see Appendix for complete species list). 60 unidentified individuals (out of 3623) were removed from the data set prior to analysis. 18 unidentified individuals occurred on annually burned plots and 42 occurred on intermittently burned plots. Unidentified individuals were immature or had experienced too much herbivory to confirm to genus. 1984 individuals from 88 species were recorded on annually burned and grazed plots, and 1518 individuals from 96 species were recorded on intermittently burned plots. T-tests revealed no significant differences in forb abundance or richness in annually burned and intermittently burned plots (Figure 6). Post-hoc tests of linear mixed effect models controlling for replicate found no significant differences in diversity (i.e. exponential of Shannon's diversity index, inverse of Simpson's diversity index) or evenness between annually burned and intermittently burned treatments (Table 3 and see Appendix).

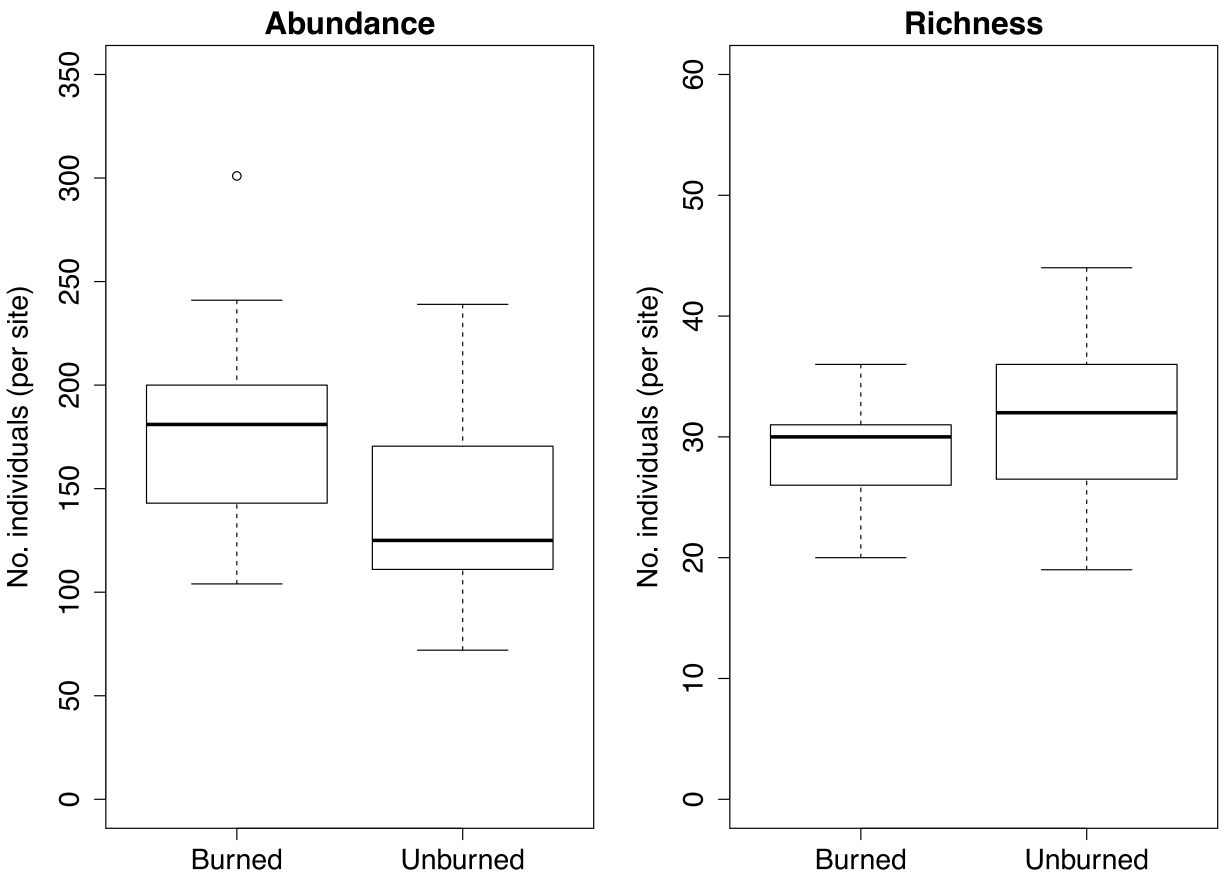

Figure 6 Mean abundance (count) and species richness of forbs per site on annually burned ('burned') and intermittently burned ('unburned') sites at Kromdraai Valley Reserve.

Table 5 Species diversity of forbs over 11 annually burned and 11 intermittently burned plots, using Hill's numbers: H_0 (average number of species per 10 m^2 plot), H_1 (exponential of Shannon's diversity index), H_2 (inverse of Simpson's diversity index), and J (Pielou's evenness). Numbers in brackets are the standard error.

Treatment	**No. of sites**	**Total no. of species**	**H_0**	**H_1**	**H_2**	**J**
Intermittently burned	11	97	32 (2.2)	17.65 (1.19)	11.31 (0.96)	0.832 (0.016)
Annually burned	11	89	29 (1.5)	15.66 (1.35)	10.48 (1.23)	0.809 (0.020)

Results of a permutational manova controlling for replicate identified elevation and aspect as significant predictors of species turnover (Table 6). Treatment (annually burned or intermittently burned) and slope were not significant predictors of species turnover.

Table 6 Permutational manova of species turnover as a function of environmental variables. Treatment refers to annually burned or intermittently burned sites.

Variable	df	Sum of Sqs	F	Pr(>F)	Significance
Elevation	1	0.0742	5.393	0.004	**
Slope	1	0.0172	1.252	0.242	
Aspect	1	0.0807	5.869	0.002	**
Treatment	1	0.0100	0.7281	0.55	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'

Of the 96 species that occurred on intermittently burned plots, two were significant indicators of treatment (Table 7). Four out of the 88 species that occurred on annually burned plots were significant indicators of treatment. The indicator species on intermittently burned plots were shade tolerant species with a preference for tall grass communities, while the indicator species on annually plots reflected a variety of life history strategies conducive to their success on grazing lawns, including vigorous reseeding (*Felicia muricata)*, high mammalian palatability (*Cyanotis speciosa)*, and lateral spread (*Chamaecrista biensis)*.

Table 7 Significant indicator values for forb species on annually burned/ intermittently burned treatments among the 22 sample sites.

Species	Treatment	Indicator value	P-value
Aloe greatheadii	Intermittently burned	0.623	0.047
Pellaea calomelanos	Intermittently burned	0.595	0.035
Felicia muricata	Annually burned	0.851	0.002
Cyanotis speciosa	Annually burned	0.689	0.022
Scabiosa columbaria	Annually burned	0.686	0.043
Chamaecrista biensis	Annually burned	0.526	0.023

3.3 Functional traits

An analysis of the height and lateral spread of the six dominant forb species did not reveal any consistent responses in functional traits across taxa. *Acalypha angustata*, *Felicia muricata, Hermannia depressa,* and *Senecio venosus* plants were significantly taller on intermittently burned plots than on annually burned plots (Figure 7). There were no significant differences in the vegetative height of *Helichrysum rugulosum* or *Scabiosa columbaria* plants. The lateral spread (diameter) of *Hermannia depressa* and *Scabiosa columbaria* plants was significantly greater on intermittently burned plots (Figure 8). There was no significant difference in lateral spread between individuals of the other four species on annually burned and intermittently burned plots.

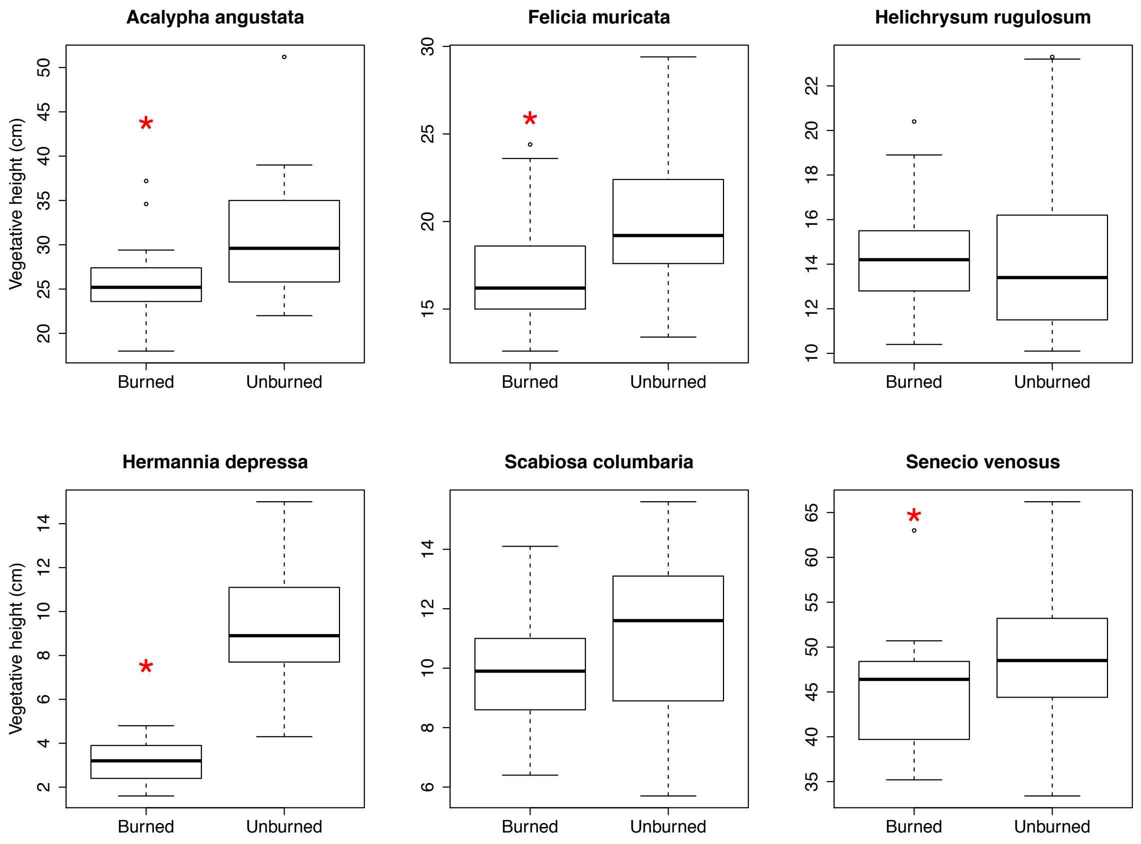

Figure 7 Vegetative height (cm) of dominant forb species on annually burned and intermittently burned sites (n=50). Significant differences between treatments are indicated by a red asterix.

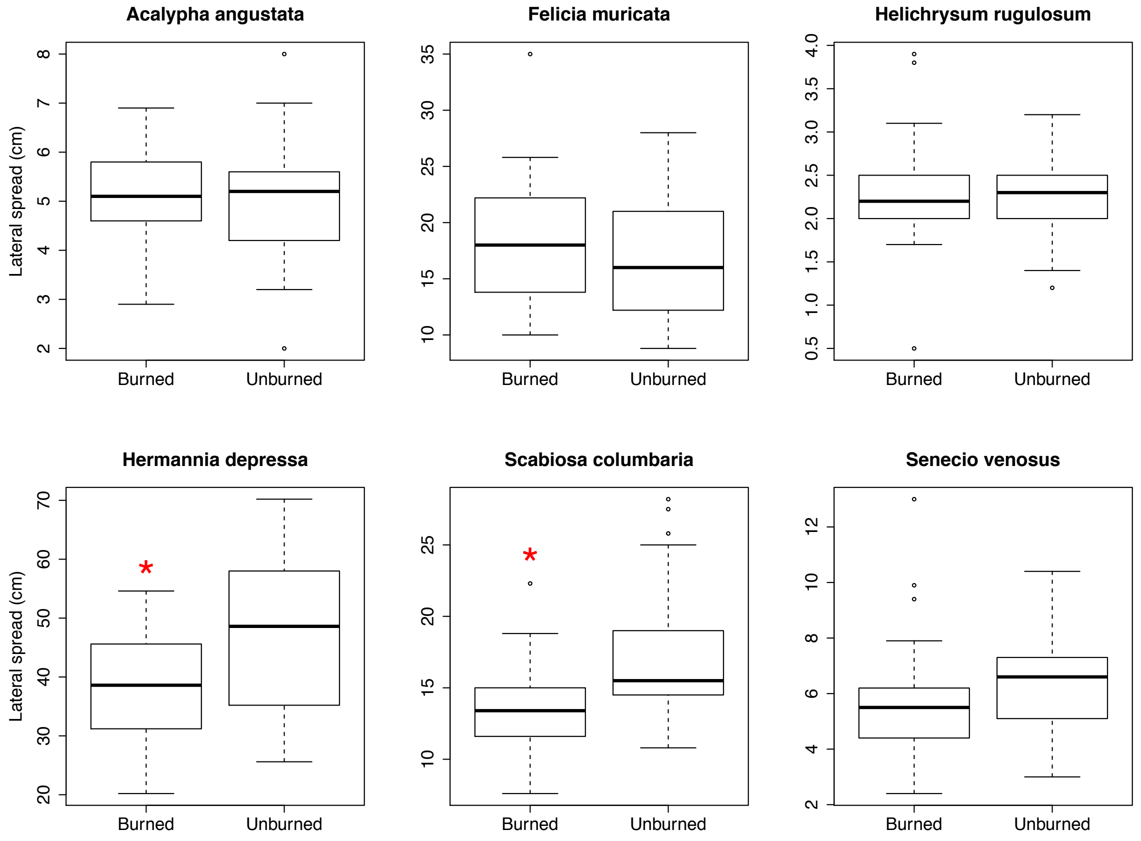

Figure 8 Lateral spread (cm) of dominant forb species on annually burned and intermittently burned sites (n=25). Significant differences between treatments are indicated by a red asterix.

An analysis of mammalian palatability score by species indicates that there were a few palatable species, though most were unpalatable. *Cyanotis speciosa*, *Pentanisia angustifolia*, and *Ledebouria sp* had palatability scores of 0.56, 0.28, and 0.22 respectively (i.e. were bitten more than n % of the time) and were the only species (of the 33 dominant species) that had a mammalian palatability score greater than 0.2 (Figure 9).

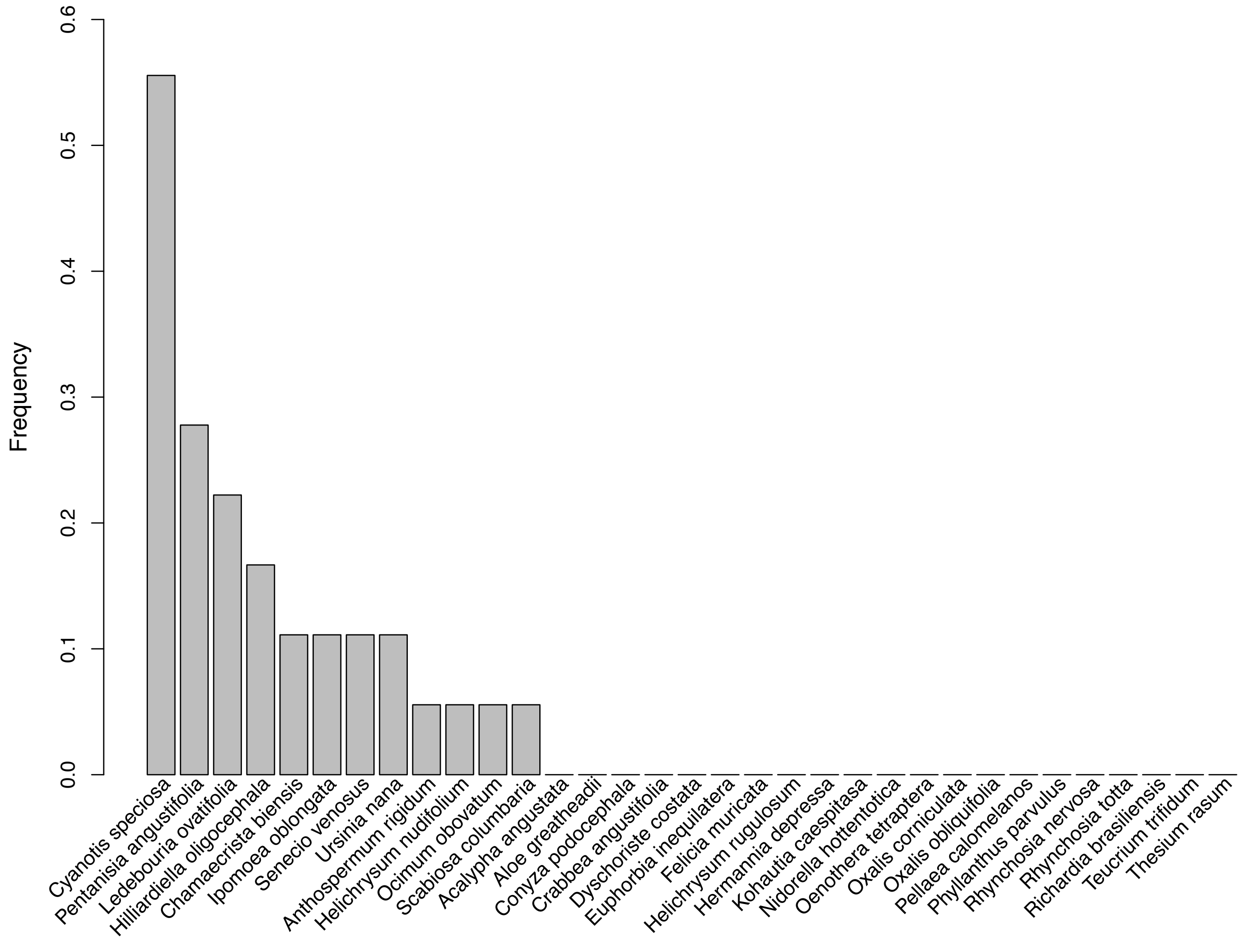

Figure 9 Mammalian palatability scores for the 33 dominant species (80% of total forb abundance). Frequency represents the probability of each species being bitten (n=18).

In contrast, an analysis of invertebrate palatability scores indicates that many species were of intermediate palatability. *Helichrysum nudifolium* and *Hermannia depressa* had the highest palatability scores (0.72 and 0.44, respectively). Of the 33 dominant species, 10 others had palatability scores greater than 0.2 (Figure 10).

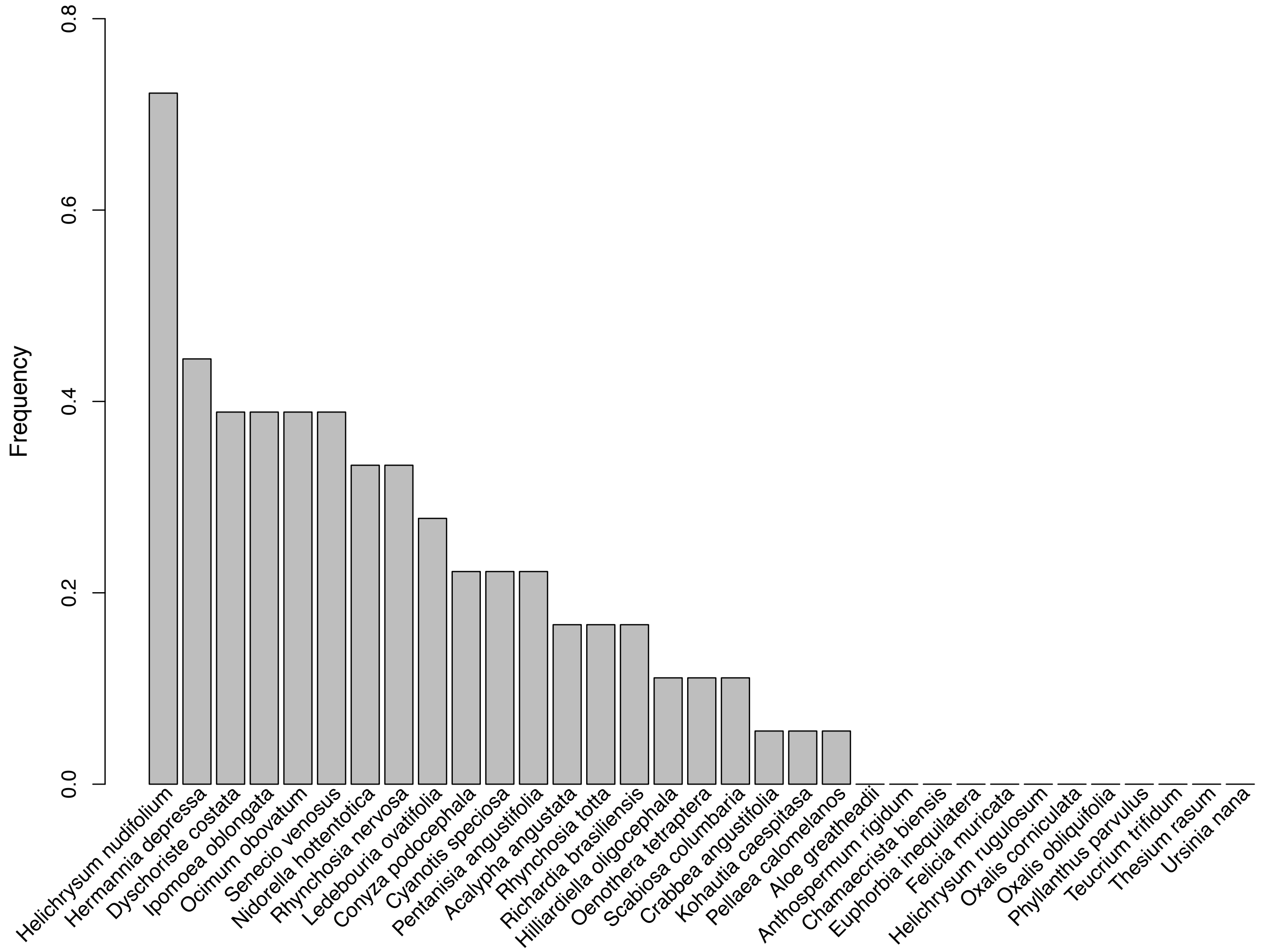

Figure 10 Invertebrate palatability scores for the 33 dominant species (80% of total forb abundance). Frequency represents the probability of each species being bitten (n=18).

3.4 Trait – environment relationship

3.4.1 Principal component analysis

The first and second principal components (PC1 and PC2) accounted for approximately 75% of the total variance in the Principal Component Analysis (PCA) (PC1 = 41%, PC2 = 34%). The annually burned and intermittently burned sites group quite clearly by grass biomass (i.e. high grass biomass on intermittently burned sites and low grass biomass on annually burned sites)

(Figure 11). The effect of replicate on grazing-related variables is also obvious, as plots with high soil moisture (C4, C5, and C11) were all on replicate B, while sites with a high penetration index/low soil compaction (C6, C7, and C8) were all on replicate C. Grass biomass had a strong negative contribution to the first principle component, while soil compaction (inverse of penetration index) and bare ground had strong positive contributions (Table 8). These trends support the inclusion of treatment as a proxy for grazing-related variables in the canonical correspondence analysis (CCA) and RLQ analysis.

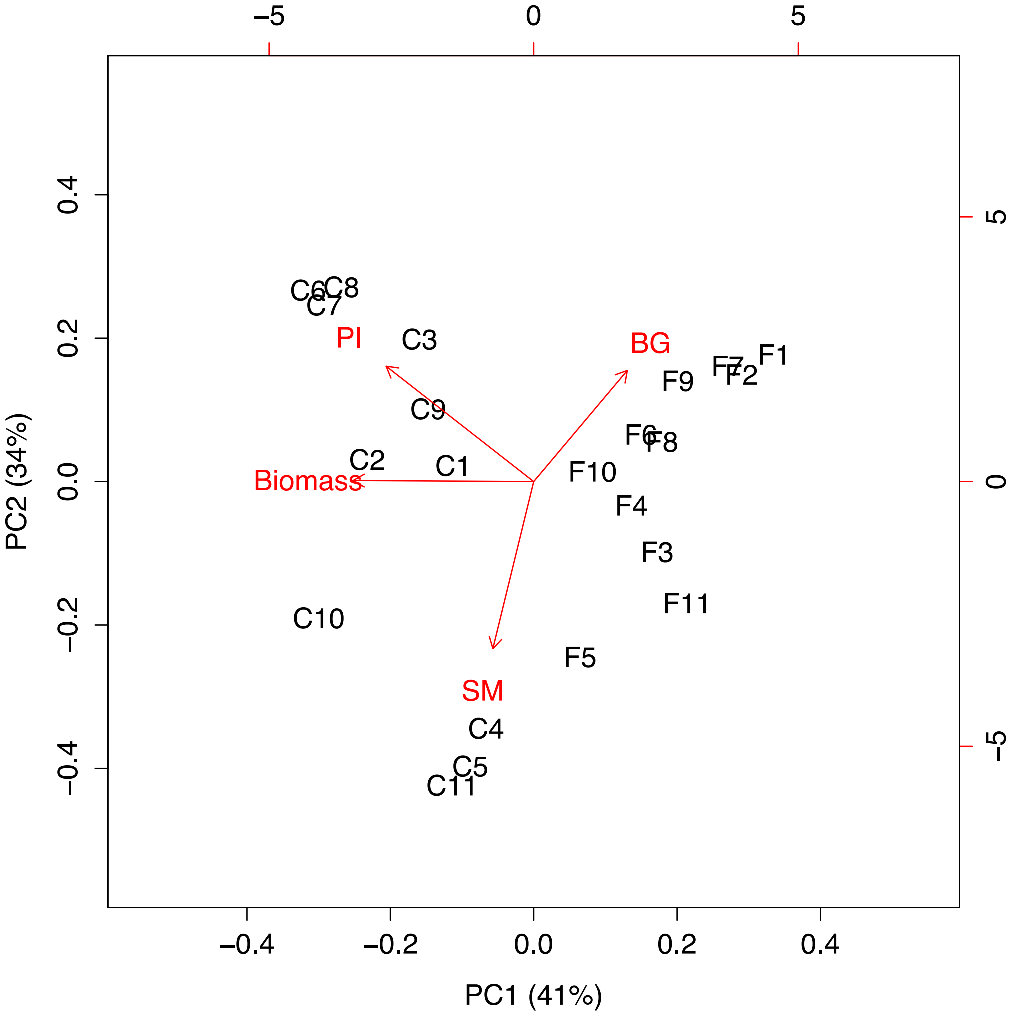

Figure 11 Outputs for the Principal Component Analysis (PCA) of grazing-related variables. Numbers in parentheses represent the percent of variation explained by each axis. C denotes control (intermittently burned) site and F denotes firebreak (annually burned) site. PI is penetration index, BG is bare ground, SM is soil moisture, and Biomass is grass biomass

Table 8 Contribution of grazing-related variables to the first four principal components (PC1, PC2, PC3, PC4).

	PC1	PC2	PC3	PC4
Soil moisture	-0.160	-0.722	0.527	-0.419
Penetration index	-0.580	0.499	-0.006	-0.644
% bare ground	0.368	0.480	0.796	0.034
Biomass	-0.709	0.005	0.298	0.639

3.4.2 Canonical correspondence analysis

A Canonical Correspondence Analysis (CCA) of the distribution of species according to environmental variables revealed that, of the environmental variables used, treatment had the greatest effect on species distribution (Figure 12). However, the signal is quite weak as the first two axes explain only 23% of the variation in species distribution. The inclusion of soil type and replicate did not improve the model. The analysis suggests that *Chamaecrista biensis* is strongly associated with annually burned treatment plots, while *Oxalis corniculata, Ledebouria sp,* and *Pentarrhinum insipidum* were strongly associated with flat, intermittently burned plots. These results are in accordance with those of the indicator value analysis (i.e. distribution of *Chamaecrista biensis*) and observations from the field.

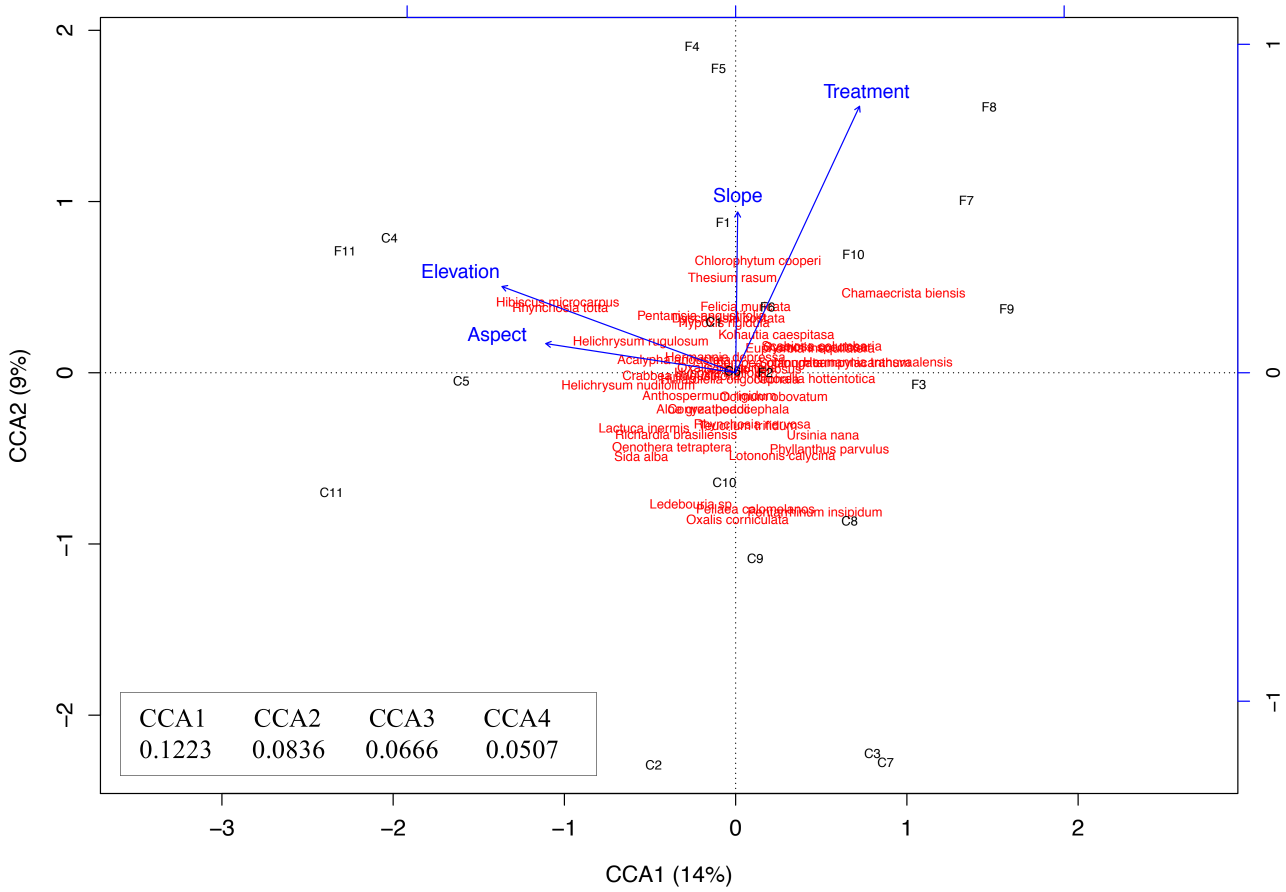

Figure 12 Canonical Correspondence Analysis (CCA) and eigenvalues for the constrained axes.

3.4.3 RLQ analysis

Table 9 gives weighted correlations of the RLQ axes with environment, demonstrating the relative contribution of each variable to forb species distribution. The first axis is negatively correlated with treatment and slope and is positively correlated with elevation and aspect. In a weighted correlation of RLQ axes with traits, the first axis is positively correlated with perennial growth form and negatively correlated with invertebrate and mammal palatability, height, and lateral spread (Table 10).

Table 9 Weighted correlations of RLQ axes with environmental variables.

Variable	**Axis 1**	**Axis 2**
TreatmentBURNED	-0.1349	0.7431
Elevation	0.9622	0.0877
Slope	-0.1116	-0.6173
AspectSOUTH	0.2381	0.3650

Table 10 Weighted correlations of RLQ axes with trait variables.

Trait	**Axis 1**	**Axis 2**
Invert	-0.3596	-0.1725
Mammal	-0.4887	0.6500
Height	-0.1319	-0.5335
Lateral spread	-0.3154	0.3235
Perennial	0.6670	0.4513

The relationship between traits and environmental variables can be represented spatially in a biplot (Figure 13). Species that were palatable for mammals were positively correlated with annually burned treatment plots, while species that were palatable for invertebrates were negatively correlated (Table 11). Shorter, more laterally spreading plants were also positively correlated with annually burned treatment plots, as were perennial species.

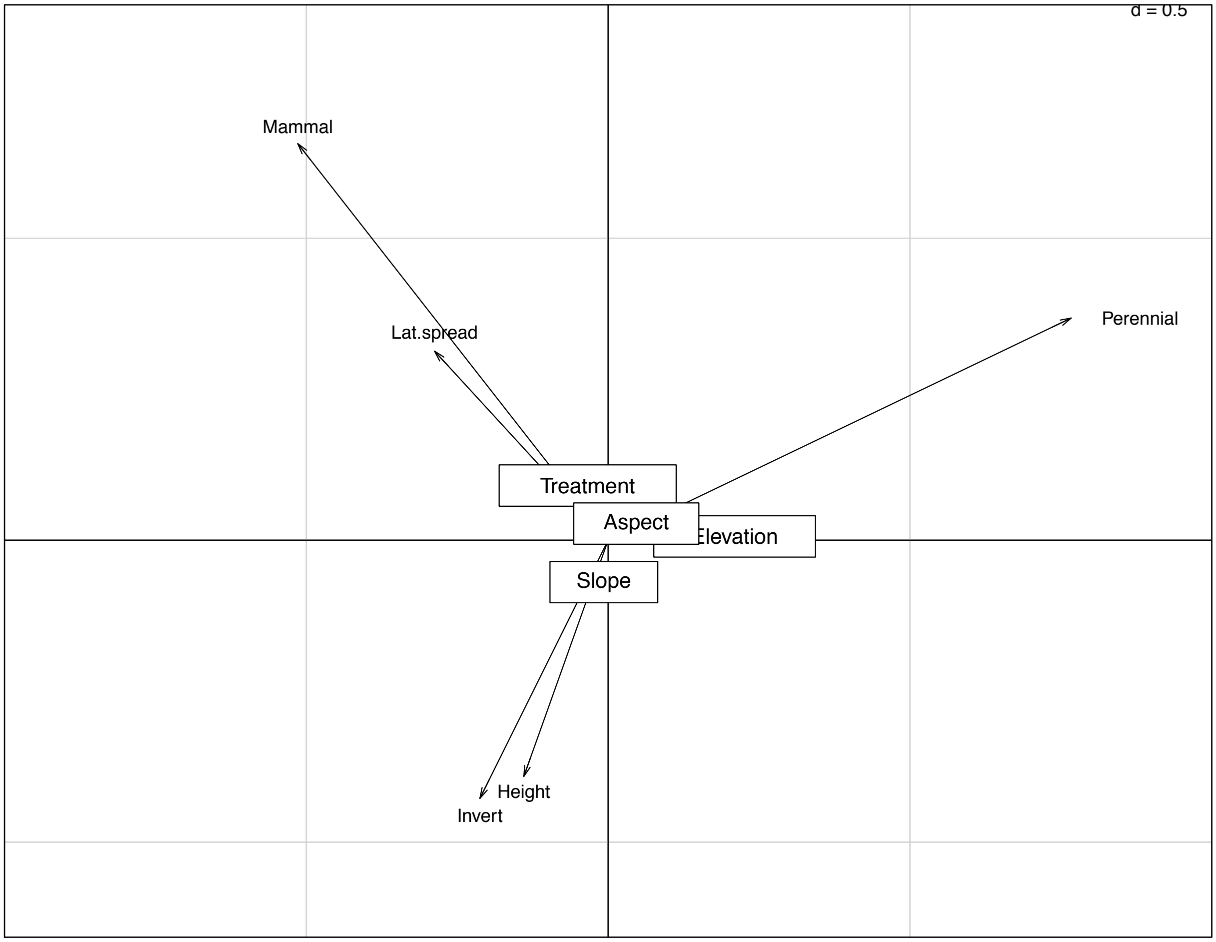

Figure 13 Biplot of trait and environmental variables.

Table 11 Correlations of traits with environment, obtained from RLQ analysis.

Variable	**Invert**	**Mammal**	**Height**	**Lateral spread**	**Perennial**
Treatment	-0.0411	0.0778	-0.0236	0.0342	0.0051
Elevation	-0.0655	-0.1090	-0.0286	-0.0588	0.1548
Slope	0.0478	-0.0308	0.0345	-0.0253	-0.0198
Aspect	0.0563	0.0201	-0.0250	-0.0061	0.0831

3.4.4 Fourth corner method

After correcting for the false discovery rate (Benjamini & Hochberg, 1995), the fourth corner analysis revealed significant associations between two of the twenty possible environment/trait correlations (Figure 14). There was a significant negative association between elevation and mammalian palatability (adjusted p-value = 0.0156) and a significant positive association between elevation and perennial growth form (adjusted p-value = 0.0024). While RLQ results indicate a positive relationship between treatment and mammalian palatability and treatment and lateral spread, these relationships were not significant.

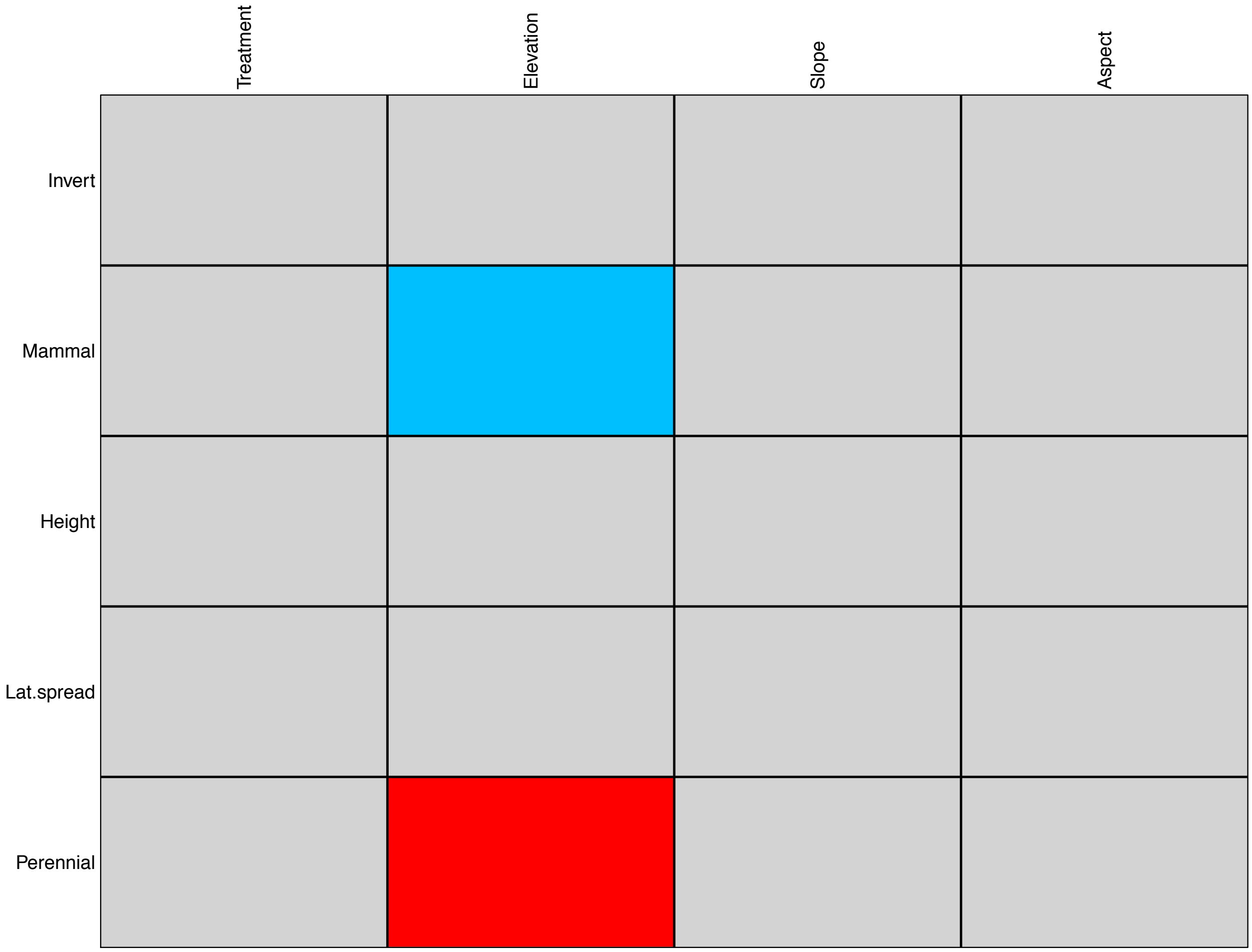

Figure 14 Fourth corner analysis for environment and trait data. Blue boxes indicate significant negative associations, while red boxes indicate significant positive associations.

4. DISCUSSION

Ten years of annual burning and heavy grazing on the firebreaks initiated little to no response in the forb community. These findings are in contrast to the original hypotheses, that 1) grazing by indigenous herbivores under current stocking rates facilitates increases in forb abundance and diversity, and 2) a unique, graze-adapted forb flora is associated with the heavily grazed firebreaks. One explanation for the absence of any significant treatment effect is that the treatment had not been applied for long enough and/or was not strong enough to initiate a response in the forb community. An alternative explanation is that forbs in the Highveld are barely grazed (Figure 9) and there is no specifically graze-adapted flora in the Highveld.

4.1 Community composition

Some degree of forb species turnover associated with treatment was expected, as there was significant turnover in the grass community at the site (F. Skhosana, unpublished data). The lack of significance in the mixed effect models indicates that even after controlling for local variation associated with firebreak position in the landscape, annual burning and heavy grazing do not cause changes in species diversity or evenness in this particular ecosystem type. McIntyre and Lavorel (2001) noted that relative to grass communities, forbs were more sensitive to topography than to grazing pressure. Their results are corroborated by this study, as permutational manovas detected significant turnover associated with elevation and aspect, rather than grazing treatment. An explanation for this is the importance of underground storage organs (USOs) for perennial forbs. USOs are not damaged by fire and enable the plant to resprout following disturbance (Uys 2006). They also make forbs less vulnerable to grazing compared to perennial grasses that retain root and shoot biomass during winter (McIntyre and Lavorel 2001). Perennial forbs accounted for more than 75% of total forb abundance at the site (Table 11), and some dominant species had prominent USOs, including *Pentanisia angustifolia, Ledebouria sp, Oxalis obliquifolia, Scabiosa columbaria* and *Cyanotis speciosa* (see Appendix). The prevalence of USOs among dominant forb species at the site and the role of USOs in resisting disturbance could explain the lack of response of the forb community to frequent fire and occasional defoliation.

A limited number of indicator species were identified for the annually burned and intermittently burned treatments, and the indicator values (measure specificity and fidelity) were generally quite low; *Felicia muricata* on annually burned plots had the highest IV of 0.851 (Table 7). Indicator species can be used to characterize site conditions in many habitats, though the indicator species identified in this analysis represent a variety of life history strategies and are not particularly useful indicators of treatment. The four indicator species for the annually burned treatments represented four different families. *Cyanotis speciosa* had an herbivory score greater than 0.5, while the other indicator species were rarely bitten. *Chamaecrista biensis* is a nodulating member of the Fabaceae family, but was the only known nitrogen-fixer among the indicator species (de Faria et al. 1989). All indicator species on annually burned and intermittently burned plots were perennial. The lack of any clear signals among indicator species corroborates the results from the diversity and turnover analyses.

The results suggest that the forb community in this high altitude mesic system responds differently to fire-grazer interactions than the grass community. A study by Zaloumis and Bond (2016), showed that it took more than 40 years to restore a grassland with forbs after plantation forestry, compared to a much shorter return-period for grasses. Similarly, Uys et al. (2004) have shown that compositional changes in grassland forb communities only occur after fire has been excluded for 10 years or more. The slow response by perennial forbs (which formed the bulk of the community) seen in other studies could explain the inability for this treatment to elicit a response in just 10 years. Additionally, the stocking rate for the reserve was relatively low with 21.7 ha LAU^{-1} versus a carrying capacity of 3 - 5 ha LAU^{-1} in high altitude grasslands (Tainton 1999). The limitations of the treatment in conjunction with the short evolutionary history of grazing could also explain the nominal impacts of the firebreak on the forb community (Milchunas et al. 1988). Data from a similar treatment in the Lowveld, where rainfall is around 600 mm pa and the evolutionary of history grazing is much longer, indicates that frequent fire and heavy grazing significantly impact the forb community (S. Archibald, unpublished data). Further studies are needed to disentangle the role of grazing history.

4.3 Functional traits

Acalypha angustata, *Felicia muricata*, *Hermannia depressa*, and *Senecio venosus* plants were significantly taller in the lightly grazed matrix. As all species were abundant on annually burned and intermittently burned plots, height differences were likely due to light limitation associated with the high grass biomass on intermittently burned plots, rather than with grazing avoidance. *Hermannia depressa* and *Scabiosa columbaria* were significantly smaller in diameter on annually burned plots, whereas a larger diameter would be expected in a grazing-adapted scenario. The smaller sizes are likely a function of increased access to light, as both these species have fleshy roots that would allow them to compete for soil moisture in scenarios of high root biomass.

Notably, the most commonly browsed forb species, *C. speciosa*, *P. angustifolia,* and *L. ovatifolia* all have large underground storage organs (particularly *P. angustifolia*, see Appendix). The high palatability of plants with USOs suggest that perhaps fire-adaptations, by definition, result in grazing adaptation. The flora of the Highveld, which is clearly adapted to fire, might be predisposed to be able to handle heavy grazing due to the dominance of perennial species. Stored reserves are required to tolerate both disturbances, as are below-ground buds and lateral growth form. Ultimately, few forb species showed signs of browsing, suggesting that much of the floral diversity was of little consequence to the herbivores at the site because; 1) other sources of food were available prior to/at the time of sampling, and/or 2) structural traits or phenotypic compounds protected many forb species from herbivory. These results may be different in times of drought. Further trait analyses should be performed to isolate phenotypic compounds that may be deterring herbivores.

4.4 Trait – environment relationship

The results of the PCA and CCA point to either little environmental determinism of species distribution, or variables that were poor representatives of environment. Little environmental determinism is more likely and is supported by the results of the community analyses, as variables included in the ordination (i.e. elevation, aspect, slope, and treatment) were comprehensive (soil texture was not included in the final model but as the sites were on one geology, is likely to correlate with elevation). More sampling sites are required to confirm the observed patterns.

As the CCA revealed little explanation of species distribution, results from the RLQ analysis must be interpreted with caution. There was a significant negative correlation between elevation and mammalian palatability (probability of being bitten), which can be explained by herbivores' preference for low-lying valleys over ridges (Kromdraai Valley Reserve, unpublished data). The significant positive correlation between elevation and perennial habit reflects the importance of storage organs for the success of perennial forbs on upper slopes that are more susceptible to drying out (McIntyre and Lavorel 2001). None of the other relationships were significant, though there is a positive association between the annually burned treatment and species that are palatable for mammals. This could point to relationship between treatment and palatability, though more sites would need to be sampled to confirm this signal.

CONCLUSION

In Kromdraai Valley Reserve, small management burns concentrate wild grazers and create heavily-grazed lawns within a lightly grazed matrix. This impacts grass community composition and increases grass productivity (F. Skhosana, unpublished data) but so far, there is no indication that small management burns have had a detectable impact on the forb communities in the reserve. All indicators of species richness and abundance showed insignificant differences between treatments (Figure 6). It should be noted that the results identified 4 species which prefer the heavily grazed and annually burned sites, and 2 species which appear to decline under these conditions (Table 5). The results also suggest that perennial species with more lateral growth forms tended to increase within the firebreaks (Table 11). Results of this study suggest that frequent fires and heavy grazing do not uniformly lead to degraded grasslands. While grazing lawns in this study attracted significantly more animals than the lightly grazed matrix, even after ten years of annual burns, the sites maintained their ecological integrity and had similar forb abundance and species richness compared to the surrounding matrix. While the frequent burning and heavy grazing treatment at the study site did not alter forb diversity, the treatment can clearly increase structural diversity, grass diversity (F. Skhosana, unpublished data), and habitat diversity for grazers in some types of Highveld grasslands.

LITERATURE CITED

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26:**32–46.

Angelo CL, Pau S. 2015. Root biomass and soil δ^{13}C in C_3 and C_4 grasslands along a precipitation gradient. Plant Ecology **216:**615–627.

Archibald S, Bond WJ. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. International Journal of Wildland Fire **13:**377-385.

Archibald S, Hempson GP. 2016 Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. Philosophical Transactions of the Royal Society B **371:** 20150309.

Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management **62:**1165–1183.

Bates D, Maechler M, Bolker B. 2011. lme4: linear mixed-effects models using S4 classes. R package version 0.999375-39. http://cran.r-project.org.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society 57:289–300.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution **24:**127–135.

Bond, WJ. 2005. Large parts of the world are brown or black: A different view on the “Green World” hypothesis. Journal of Vegetation Science **16:**261–266.

Bond WJ, Keeley JE. 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution **20:**387–394.

Bowman DMJS, Perry GLW, Higgins SI, Johnson CN, Fuhlendorf SD, Murphy BP. 2016. Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. Philosophical Transactions of the Royal Society B **371:** 20150169.

Bransby DI, Tainton NM. 1977. The disc pasture meter: Possible applications in grazing management. Proclamations of the Grassland Society of South Africa **12:** 115–118.

Bullock JM, Franklin J, Stevenson MJ, Silvertown J, Coulson SJ, Gregory SJ, Tofts R. 2001. A plant trait analysis of responses to grazing in a long-term experiment. Journal of Applied Ecology **38:**253–267.

Burkepile DE, et al. 2016. Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna. Oikos **000:**1–11. doi: 10.1111/oik.02987.

Cingolani AM, Posse G, Collantes MB. 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. Journal of Applied Ecology **42:**50–59.

Coe MJ, Cumming DH, Phillipson J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia **22:**341–354.

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280:**745-747.

Collins SL, Smith MD. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology **87:**2058-2067.

Cornelissen JHC, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany **51:**335–380.

de Faria SM, Lewis GP, Sprent JI, Sutherland JM. 1989. Occurrence of nodulation in the Leguminosae. New Phytologist **111:**607–619.

Díaz S, et al. 2007. Plant trait responses to grazing -- a global synthesis. Global Change Biology **13:**313–341.

Dray S, Chessel D, Thioulouse J. 2003 Co-inertia analysis and the linking of ecological data tables. Ecology **84:**3078-3089.

Dray S, Dufour AB. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software **22:**1–20.

Dray S, Holer PHC, Ole SYD. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology **95:**14–21.

Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67:**345–366.

Eloff G. 2010. The phytosociology of the natural vegetation occurring in the Cradle of Humankind world heritage site, Gauteng. South Africa. M.Sc. thesis, University of South Africa, South Africa.

Fuhlendorf SD, Engle DM, Kerby J, Hamilton R. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology **23:**588–598.

Germishuizen, G, Meyer NL. 2003. Plants of Southern Africa: an annotated checklist (Strelitzia no. 14). South African National Biodiversity Institute, Pretoria.

Hayes GF, Holl KD. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. Conservation Biology **17:**1694–1702.

Hempson GP, et al. 2015. Ecology of grazing lawns in Africa. Biological Reviews **90:**979–994.

Hickman KR, Hartnett DC. 2002. Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. Plant Ecology **159:**23–33.

Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology **54:**427–432.

Hilton-Barber B, Berger LR. 2004. Field guide to the cradle of humankind: Sterkfontein, Swartkrans, Kromdraai and Environs World Heritage Site. Struik.

Hothorn T, Bretz F, Westfall P, Heiberger RM. 2008. multcomp: simultaneous inference for general linear hypotheses. R package version 0.993-1. http://CRAN.R-project.org.

Kattge J, et al. 2011 TRY–a global database of plant traits. Global Change Biology **17:**2905-2935.

Knapp AK, et al. 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. Journal of Plant Ecology **5:**357-365.

Langevelde F, et al. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology **84:**337–350.

Legendre P, Galzin R, Harmelin-Vivien ML. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology **78:**547-562.

Little IT, Hockey PAR, Jansen R. 2015. Impacts of fire and grazing management on South Africa’s moist highland grasslands: A case study of the Steenkampsberg Plateau, Mpumalanga, South Africa. Bothalia (45) http://dx.doi.org/10.4102/abc. v45i1.1786.

McArdle BH, Anderson MJ. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology **82:**290–297.

McIntyre S, Lavorel S. 2001. Livestock grazing in sub- tropical pastures: steps in the analysis of attribute response and plant functional types. Journal of Ecology **89:**209-226.

McNaughton SJ. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist **113:**691-703.

McNaughton SJ. 1984. Grazing Lawns: animals in herds, plant form, and coevolution. The American Naturalist **124:**863–886.

McNaughton SJ, Ruess RW, Seagle SW. 1988. Large mammals and process dynamics in African ecosystems. BioScience **38:**794–800.

Milchunas DG, Sala OE, Lauenroth WK. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist **132:**87–106.

Mucina, et al. 2006. Grassland Biome. Pages 349–436 in Mucina L, Rutherford MC, editors. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute (SANBI), Pretoria.

Norton-Griffiths M. 1995. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 310–352 in Sinclair ARE, Norton-Griffiths M, editors. Serengeti: Dynamics of an ecosystem. 2nd edition. University of Chicago Press, Chicago.

Noy-Meir I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. Journal of Vegetation Science **6:**701-710.

Oksanen J, et al. 2013. Vegan: Community ecology package. R package version 2. 0–10. http://CRAN.R-project.org/package=vegan.

Owen-Smith N, Cooper SM. Nutritional ecology of a browsing ruminant, the kudu (Tragelaphus strepsiceros), through the seasonal cycle. Journal of Zoology **219.1:**29-43.

Pakeman RJ, Quested HM. 2007. Sampling plant functional traits: what proportion of the species need to be measured? Applied Vegetation Science **10:**91–96.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts DW. 2013. labdsv: ordination and multivariate analysis for ecology. R package version 1.6-1. http.CRAN. R-project.org/package= labdsv.

Rowe-Rowe DT, Scotcher JSB. 1986. Ecological carrying capacity of the Natal Drakensberg for wild ungulates. South African Journal of Wildlife Research **16:**12-16.

Scott-Shaw R, Morris CD. 2014. Grazing depletes forb species diversity in the mesic grasslands of KwaZulu-Natal, South Africa. African Journal of Range & Forage Science **0119:**1–11.

Sensenig RL, Demment MW, Laca EA. 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology **91:**2898–2907.

Siebert F, Scogings P. 2015. Browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence. South African Journal of Botany **100:**69–74.

Siebert F and Siebert SJ. 2005. Dolomitic vegetation of the Sterkfontein Caves World Heritage Site and its importance in the conservation of Rocky Highveld Grassland. Koedoe **48:**17–31.

Skhosana FV. 2015. Fire-grazer interactions in a highveld grassland. M.Sc. proposal, University of the Witwatersrand, Johannesburg.

South African National Biodiversity Institute. 2016. Botanical Database of Southern Africa (BODATSA). doi: to be assigned.

Stohlgren TJ, Falkner MB, Schell LD. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117:**113–121.

Tainton NM, Mentis MT. 1984. Fire in grassland. Pages 115-147 in de Booysen PV, Tainton NM, editors. Ecological effects of fire in South African ecosystems. Springer Berlin, Heidelberg.

Tainton NM. 1999. Veld management in South Africa. University of Natal Press, Pietermaritzburg.

Uys RG, Bond WJ, Everson TM. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. Biological Conservation **118:**489–499.

Uys RG. 2006. Patterns of plant diversity and their management across South African Rangelands. Ph.D thesis, University of Cape Town, Cape Town.

Van Coller H, Siebert F, Siebert SJ. 2013. Herbaceous species diversity patterns across various treatments of herbivory and fire along the sodic zone of the Nkuhlu exclosures, Kruger National Park. Koedoe **55:**1–6.

Van Wilgen BW, Scholes RJ. 1997. The vegetation and fire regimes of southern hemisphere Africa. Pages 27–46 in van Wilgen BW, Andreae MO, Goldammer JG, Lindesay JA, editors. Fire in Southern African savannas: Ecological and atmospheric perspectives. Witwatersrand University Press, Johannesburg.

Van Wyk B, Malan S. 1997. Field guide to the wild flowers of the Highveld. 2nd edition. New Holland Publishers, Cape Town.

Verweij RJT, Verrelst J, Loth PE, Heitkönig IMA, Brunsting AMH. 2006. Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. Oikos **114:**108-116.

Waldram MS, Bond WJ, Stock WD. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African Savanna. Ecosystems **11:**101–112.

Zaloumis NP, Bond WJ. 2016. Reforestation or conservation? The attributes of old growth grasslands in South Africa. Philosophical Transactions of the Royal Society B **371:**20150310.

APPENDIX

Table 1 Species counts on and off firebreaks at Kromdraai Valley Reserve. A star in the dominant column indicates that the species composed 80% of total forb abundance and was included in trait analyses (South African National Biodiversity Institute 2016).

		Count			
Family	**Species**	**Annually burned**	**Intermittently burned**	**Total**	**Dominant**
Acanthaceae	Blepharis integrifolia	22	11	33	
Acanthaceae	Crabbea angustifolia	23	31	54	*
Acanthaceae	Dyschoriste costata	20	19	39	*
Agavaceae	Chlorophytum cooperi	11	4	15	
Agavaceae	Chlorophytum transvaalense	1	4	5	
Amaranthaceae	Gomphrena celosioides	0	2	2	
Amaryllidaceae	Boophane disticha	1	0	1	
Anacardiaceae	Searsia sp	0	2	2	
Apocynaceae	Asclepias affinis	1	2	3	
Apocynaceae	Pentarrhinum insipidum	1	13	14	
Apocynaceae	Raphionacme hirsuta	6	2	8	
Asparagaceae	Asparagus suaveolens	2	0	2	
Asphodelaceae	Aloe greatheadii	27	61	88	*
Asphodelaceae	Trachyandra sp	0	1	1	
Asteraceae	Athrixia elata	0	7	7	
Asteraceae	Conyza podocephala	38	46	84	*
Asteraceae	Felicia muricata	262	47	309	*
Asteraceae	Gazania krebsiana	2	1	3	
Asteraceae	Geigeria burkei	2	0	2	
Asteraceae	Gerbera piloselloides	2	6	8	
Asteraceae	Helichrysum caespititium	4	2	6	
Asteraceae	Helichrysum callicomum	8	16	24	
Asteraceae	Helichrysum cephaloideum	4	1	5	
Asteraceae	Helichrysum nudifolium	6	34	40	*
Asteraceae	Helichrysum rugulosum	186	193	379	*
Asteraceae	Helichrysum setosum	0	3	3	
Asteraceae	Hilliardiella oligocephala	47	26	73	*
Asteraceae	Lactuca inermis	2	10	12	
Asteraceae	Launaea rarifolia	0	5	5	
Asteraceae	Nidorella hottentotica	63	38	101	*

Asteraceae	Nolletia rarifolia	13	4	17	
Asteraceae	Senecio coronatus	3	1	4	
Asteraceae	Senecio oxyrifolius	1	0	1	
Asteraceae	Senecio venosus	104	96	200	*
Asteraceae	Seriphium plumosum	2	6	8	
Asteraceae	Sonchus maratimus	1	10	11	
Asteraceae	Tagetes minuta	3	15	18	
Asteraceae	Tolpis capensis	2	5	7	
Asteraceae	Ursinia nana	26	11	37	*
Caryophyllaceae	Dianthus mooiensis	0	1	1	
Caryophyllaceae	Pollichia campestris	0	6	6	
Chrysobalanaceae	Parinari capensis	6	7	13	
Commelinaceae	Cyanotis speciosa	80	16	96	*
Convolvulaceae	Convolvulus sagittatus	1	0	1	
Convolvulaceae	Ipomoea oblongata	24	11	35	*
Cucurbitaceae	Cucumis zeyheri	1	0	1	
Cyperaceae	Cyperaceae sp	2	13	15	
Cyperaceae	Cyperus obtusiflorus	0	2	2	
Cyperaceae	Cyperus rupestris	3	4	7	
Dipsacaceae	Scabiosa columbaria	155	30	185	*
Ebenaceae	Diospyros lycioides	1	7	8	
Euphorbiaceae	Acalypha angustata	107	128	235	*
Euphorbiaceae	Euphorbia inequilatera	34	14	48	*
Fabaceae	Chamaecrista biensis	27	1	28	*
Fabaceae	Dolichos angustifolius	0	1	1	
Fabaceae	Elephantorrhiza elephantina	0	5	5	
Fabaceae	Indigofera hilaris	3	5	8	
Fabaceae	Lotononis calycina	6	14	20	
Fabaceae	Lotononis listii	10	3	13	
Fabaceae	Rhynchosia nervosa	10	31	41	*
Fabaceae	Rhynchosia totta	11	15	26	*
Fabaceae	Sphenostylis angustifolia	1	6	7	
Fabaceae	Tephrosia elongata	0	2	2	
Fabaceae	Tephrosia subglabra	0	2	2	
Geraniaceae	Monsonia angustifolia	8	3	11	
Hyacinthaceae	Eucomis autumnalis	0	1	1	
Hyacinthaceae	Ledebouria sp	3	15	18	*
Hyacinthaceae	Ornithogalum tenuifolium	0	2	2	
Hypoxidaceae	Hypoxis argentea	4	9	13	

Hypoxidaceae	Hypoxis iridifolia	7	4	11	
Hypoxidaceae	Hypoxis rigidula	9	7	16	
Iridaceae	Moraea simulans	3	1	4	
Lamiaceae	Ocimum obovatum	20	15	35	*
Lamiaceae	Salvia runcinata	3	3	6	
Lamiaceae	Teucrium trifidum	25	31	56	*
Malvaceae	Corchorus asplenifolius	21	6	27	
Malvaceae	Hermannia depressa	191	122	313	*
Malvaceae	Hermannia transvaalensis	10	4	14	
Malvaceae	Hibiscus aethiopicus	2	7	9	
Malvaceae	Hibiscus microcarpus	7	7	14	
Malvaceae	Sida alba	4	8	12	
Malvaceae	Sida dregei	0	3	3	
Oleaceae	Menodora africana	1	1	2	
Onagraceae	Oenothera tetraptera	5	18	23	*
Orobanchaceae	Graderia subintegra	1	0	1	
Oxalidaceae	Oxalis corniculata	1	21	22	*
Oxalidaceae	Oxalis obliquifolia	24	28	52	*
Phyllanthaceae	Phyllanthus parvulus	22	26	48	*
Polygalaceae	Polygala hottentotta	0	4	4	
Polygonaceae	Rumex sp	14	0	14	
Pteridaceae	Pellaea calomelanos	4	19	23	*
Rhamnaceae	Ziziphus zeyheriana	17	23	40	
Rubiaceae	Anthospermum rigidum	14	14	28	*
Rubiaceae	Kohautia amatymbica	11	3	14	
Rubiaceae	Kohautia caespitasa	34	13	47	*
Rubiaceae	Pentanisia angustifolia	12	24	36	*
Rubiaceae	Richardia brasiliensis	48	54	102	*
Santalaceae	Thesium rasum	36	14	50	*
Santalaceae	Thesium sp	10	2	12	
Solanaceae	Solanum campylacanthum	16	2	18	
Solanaceae	Solanum elaeagnifolium	4	3	7	
Thymelaeaceae	Gnidia sericocephala	2	1	3	
Verbenaceae	Lippia javenica	10	3	13	
Verbenaceae	Verbena aristigera	2	0	2	
Verbenaceae	Verbena brasiliensis	1	1	2	
	Total	**1984**	**1581**	**3565**	

Table 2 Mixed models of diversity indices, controlling for replicate as a random factor.

Model	z value	Pr(>|z|)
M1 = lmer(H0 ~ Treatment + (1|Replicate))	1.151	0.25
M2 = lmer(H1 ~ Treatment + (1|Replicate))	1.212	0.226
M3 = lmer(H2 ~ Treatment + (1|Replicate))	0.612	0.54
M4 = lmer(J ~ Treatment + (1|Replicate))	0.993	0.321

Figure 1 Underground storage organ (USO) of *Pentanisia angustifolia*

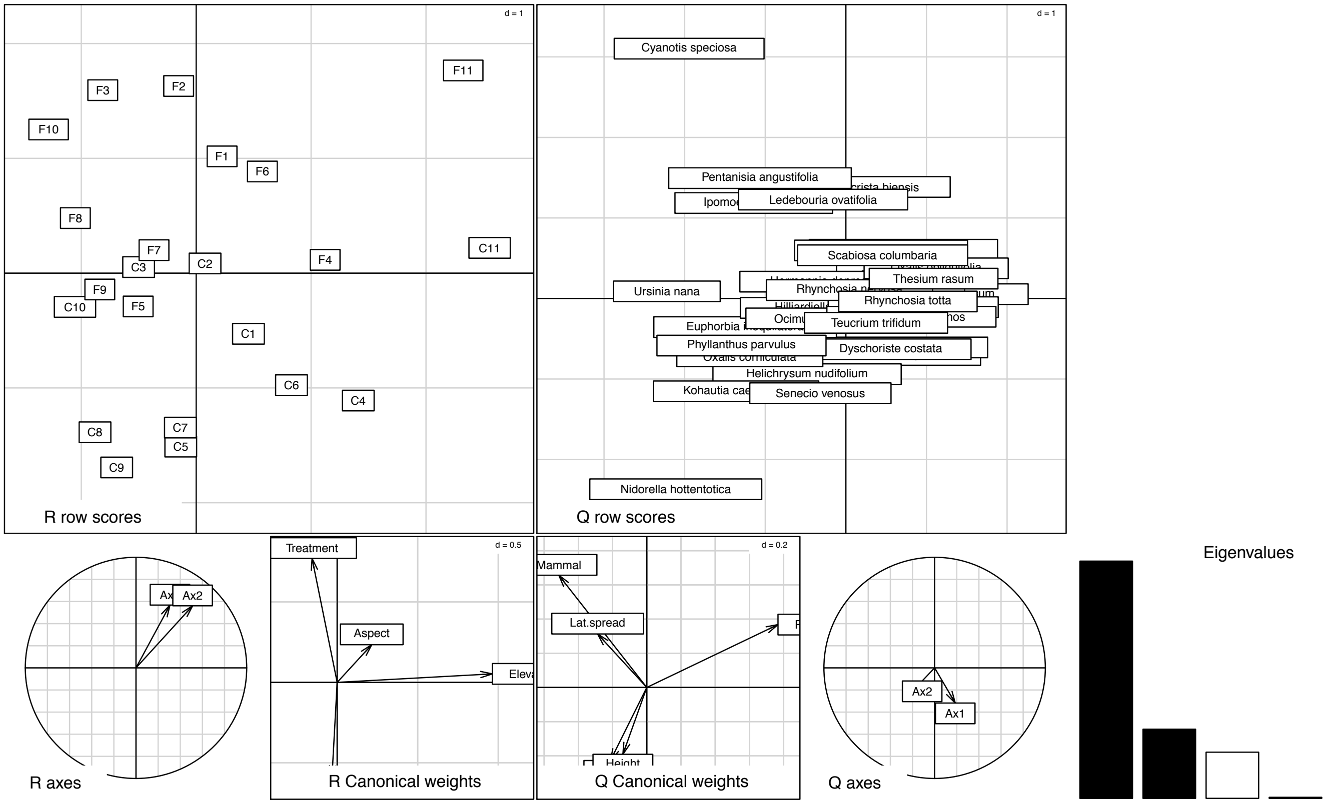

Figure 2 Main outputs obtained from RLQ analysis.

Table 3 Summary of outputs from the fourth corner method, which was adjusted for multiple comparisons using the false discovery rate (fdr) method.

Relationship			Test Stat	Obs	Std.Obs	Pvalue	Pvalue.adj	Significance
Treatment	/	Invert	r	-0.041	-1.121	0.263	0.585	
Elevation	/	Invert	r	-0.066	-1.788	0.074	0.296	
Slope	/	Invert	r	0.048	1.301	0.193	0.482	
Aspect	/	Invert	r	0.056	1.532	0.125	0.357	
Treatment	/	Mammal	r	0.078	2.201	0.027	0.177	
Elevation	/	Mammal	r	-0.109	-3.056	0.002	0.016	*
Slope	/	Mammal	r	-0.031	-0.863	0.396	0.648	
Aspect	/	Mammal	r	0.020	0.563	0.579	0.681	
Treatment	/	Height	r	-0.024	-0.646	0.518	0.648	
Elevation	/	Height	r	-0.029	-0.793	0.432	0.648	
Slope	/	Height	r	0.035	0.958	0.339	0.616	
Aspect	/	Height	r	-0.025	-0.689	0.490	0.648	
Treatment	/	Lat.spread	r	0.034	0.971	0.333	0.616	
Elevation	/	Lat.spread	r	-0.059	-1.667	0.095	0.318	
Slope	/	Lat.spread	r	-0.025	-0.714	0.477	0.648	
Aspect	/	Lat.spread	r	-0.006	-0.177	0.859	0.900	
Treatment	/	Perennial	r	0.005	0.130	0.900	0.900	
Elevation	/	Perennial	r	0.155	3.817	0.000	0.002	**
Slope	/	Perennial	r	-0.020	-0.488	0.632	0.702	
Aspect	/	Perennial	r	0.083	2.062	0.039	0.194	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1