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Fire and herbivory control shrub encroachment and restore herbaceous vegetation in mesic grasslands of South Africa

Mthunzi Mndela ^{a,b}, Alan S. Barrett  ^b and Leslie R. Brown  ^b

^aDepartment of Livestock and Pasture Science, University of Fort Hare, Alice, South Africa; ^bApplied Behavioural Ecology and Ecosystem Research Unit, Department of Environmental Science, University of South Africa, Florida, Republic of South Africa

ABSTRACT

Background: Shrub encroachment suppresses ecosystem services of grasslands. Hence, the impact of herbivory and fire as shrub control measures needs to be ascertained for restoration of mesic grasslands.

Objective: To assess the impact of fire and wild ungulates on controlling *Seriphium plumosum* encroachment and restoration of herbaceous vegetation.

Methods: Four 50 m × 25 m blocks were selected randomly in a large shrub-encroached site, with blocks demarcated at least 1 km apart in the Telperion Nature Reserve, South Africa. Half of each block was fenced off to exclude wild herbivores (enclosure) and the adjacent half was unfenced (non-enclosure). Two blocks burned in 2020, resulting in the following treatments: fire, herbivory, fire and herbivory combination, and no fire no herbivory. In each treatment, thirty-two 4 m × 4 m subplots were nested to repeatedly survey shrub and herbaceous vegetation.

Results: Herbaceous plant density, diversity, richness, and basal cover declined linearly with increase in shrub cover. All treatments significantly reduced shrub cover, with fire in combination with herbivory reducing it nearly three-fold compared to that in the control. Plant densities and species richness were higher in the treatment with fire and herbivory than in the other treatments, or in the control. For all treatments, the herbaceous canopy cover and diversity were comparable, but significantly higher than in the control.

Conclusions: Our findings indicate that integration of burning, and herbivory is best for controlling shrub encroachment and restoration of herbaceous vegetation in mesic grasslands.

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Burning; herbaceous cover; mesic grasslands; plant density; shrub encroachment; species diversity and richness; wild herbivores

Introduction

The Grassland Biome which covers 28% of South Africa has a high floristic and mammal diversity and is utilised primarily for grazing (Mucina and Rutherford 2006). South African grasslands comprise largely of mesic and semi-arid grasslands, with the former occurring in regions receiving annual rainfall of above 600 mm while the latter occur in semi-arid regions with annual rainfall of 200 to 600 mm (Fynn and O'Connor 2005; Yves et al. 2012). The physiognomic structure of this biome such as grass dominance is maintained by fire and grazing (Fynn and O'Connor 2005). Recently, approximately 40% of this biome has been transformed into other land uses, with large parts of the remaining 60% subjected to shrub encroachment due to changes in fire and grazing regimes (Graham et al. 2020). Shrub encroachment refers to an increase in the density, cover, and biomass of shrubs to the detriment of the herbaceous layer, owing to complex interactions of climate change, overgrazing, elevated atmospheric CO₂ and reduced fire frequencies and intensity (Abercrombie et al. 2019; Mndela et al. 2022a, 2023a).

In South Africa, a dwarf and multi-stemmed shrub, *Seriphium plumosum* (Bankrupt bush) has encroached in many grasslands including seven of the nine provinces, predominantly Eastern Cape, Free State, Mpumalanga, North-West and Gauteng Provinces (Urban et al. 2021). Of the 17 million hectares of rangelands in South Africa, 10% is encroached by *S. plumosum*, largely Grasslands and Savanna biomes (Department of Agriculture, Forestry and Fisheries 2019). Although not as vigorous as in South Africa, *S. plumosum* encroaches in rangelands of Mozambique, Zimbabwe, Namibia (Germishuizen and Meyer 2003), and Madagascar (Schmidt et al. 2002; Badenhorst 2009). The encroachment of this shrub is characteristic of vegetation degradation (Wepener 2007), as it suppresses herbaceous cover, diversity, and production, leading to biodiversity loss and a decline in grazing capacity (Nkosi et al. 2018; Marquart et al. 2022). These vegetation changes are a consequence of competition for light, soil nutrients and moisture imposed by shading from the canopy and vigorous root system of the shrub (Van Zyl and Avenant 2018). The roots of *S. plumosum* can grow as

CONTACT Leslie R. Brown  L.R.Brown@unisa.ac.za

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deep as 1.8 m, with root biomass remaining highest in the subsurface, which enhances its nutrient and moisture uptake relative to shallow rooted grasses (Avenant 2015).

Seriphium plumosum encroaches intensively where herbaceous cover is denuded, predominantly in overgrazed rangelands or abandoned croplands due to low shrub-grass competition during early successional stages of vegetation recovery (Clark et al. 2020; Snyman 2012). The increase in *S. plumosum* encroachment appears to be exacerbated, in part, by its high production of wind-dispersed seeds and colonisation of nutrient-poor soils (Snyman 2010; Mndela et al. 2023a). Approximately 65% of seeds can retain viability and germinate three years after seed set, thereby increasing the density of this shrub (Snyman 2010). Intervention strategies to mitigate shrub encroachment are crucial to facilitate herbaceous vegetation recovery (Liao et al. 2018). The success of these interventions can be guided by the knowledge of rangeland management paradigms including amongst others plant succession and state-and-transition models (Briske 2017). Understanding these rangeland management paradigms may inform a determination of whether passive vegetation recovery following shrub management is adequate or active restoration is necessary. The plant succession framework suggests that an increase in shrub abundance is a state within a continuous process, heading towards single climax state (Jeltsch et al. 2000). This model posits that the shrub-encroached state is reversible to grassland state upon imposing disturbance e.g. browsing or fire (Briske et al. 2003). Thus, the shrub encroachment phenomenon is a result of low browsing herbivore populations and reduced fire frequencies (Liao et al. 2018).

The plant succession model, however, overlooks the existence of the threshold between two stable states, beyond which reversibility of shrubland to pre-encroachment state would be impossible without high input interventions, e.g. mechanical removal of shrubs (Briske 2017; Liao et al. 2018). The development of state-and-transition model, which is inclusive of threshold concept (Westoby et al. 1989), opened new avenues to reconsider and redefine shrub management interventions for land users (Liao et al. 2018). The state-and-transition model suggests that vegetation dynamics are characterised by discrete states, separated by discrete transitions and thresholds, which if surpassed the reversibility to the previous state requires shrub clearing (Briske et al. 2005). For instance, in some rangelands, extended periods of fire exclusion have allowed woody plants to establish such that even if burning is reinstated, it becomes ineffective as the threshold of 40% shrub cover has already been surpassed (Roques et al. 2001). However, a potential of integrated fire and herbivory to reverse

encroachment of a highly flammable *S. plumosum* has not been assessed for management of mesic grasslands (Du Toit 2012; Van Zyl and Avenant 2018). Fire and herbivory are an integral component of grasslands, driving ecosystem processes and functioning (Malongweni and Van Tol 2022). These disturbances, independently or via interactions, shape grassland vegetation structure by suppressing shrub cover and open space for grasses to dominate (Malongweni and Van Tol 2022). Ungulates through browsing and trampling together with fire kill seedlings and adult shrubs, creating conditions suitable for herbaceous plant recruitment (Venter et al. 2017; O'Connor et al. 2020).

Although fire and herbivory interact to influence vegetation dynamics, singularly, they impose differential effects on vegetation structure and composition, as these selective pressures select for differential plant adaptive traits (Huang et al. 2018). Herbivory via trampling, grazing and defaecation promotes niche heterogeneity, giving rise to diverse communities with species exhibiting interspecific niche preference (Marion et al. 2010). Nevertheless, inappropriate grazing regimes, e.g. overgrazing, especially after fire, may denude herbaceous cover and amplify soil erosion (Cingolani et al. 2013). Similarly, non-prescribed wild-fires of high intensity may be detrimental to native fire-sensitive species, leading to declines in herbaceous plant density, diversity, and cover (Emery and Gross 2005).

High-intensity fires particularly during dry season are expected in grasslands encroached by *S. plumosum*, as the shrub contains volatile oils (Van Zyl and Avenant 2018). In contrast, in fire-prone ecosystems, such as most grasslands in Southern Africa, herbaceous species are highly resilient to frequent fires and may persist longer and dominate the system, as most species co-evolved with fire (Phillips 2012; Huang et al. 2018; Mndela et al. 2023c). These plant species apply certain adaptive strategies, e.g. synchronous flowering (Fontenele et al. 2020; Mndela et al. 2023c) and resprouting from crown, rhizomes and geoxyllic suffrutex stems (Maurin et al. 2014; Simpson et al. 2021; Mndela et al. 2023b).

Fire and herbivory interactions, also referred to as pyric herbivory, occur via a mechanism referred to by Archibald et al. (2005) as 'magnet effect' in which herbaceous plants regrowth attracts ungulate herds to burned areas. Depending on the fire and herbivory regimes, pyric herbivory may drive shifts in community structure and composition to the dominance of short-statured grasses due to additive effects of herbivory (Donalson et al. 2017). A worst-case scenario could be the loss of native fire-intolerant herbaceous species and the increase of exotic herbaceous invaders (Emery and Gross 2005). An in-depth understanding of the effects of

fire and herbivory, either acting singularly or together on herbaceous vegetation, is required to devise management and vegetation restoration strategies for mesic grasslands.

This study answered the following questions: 1) how herbaceous cover, diversity, density, and richness would decline to respond along an increasing gradient of *S. plumosum* cover, 2) if the use of fire and herbivory reverse *S. plumosum* encroachment, and 3) if the use of fire and herbivory affects herbaceous vegetation in mesic grasslands. We hypothesised that herbaceous cover, diversity, density, and species richness would decline with increase in *S. plumosum* cover, and that fire and herbivory, alone and in combination, would reduce *S. plumosum* cover and facilitate herbaceous vegetation recovery.

Materials and methods

Site description

The study was conducted at Telperion Nature Reserve (TNR) in the Mpumalanga Province of

South Africa (Figure 1). The reserve is situated 25 km east of Bronkhorstspruit town, east of Pretoria and it covers an extent of 11 000 ha. Telperion is 1350 m above sea level. The mean annual rainfall at TNR ranges from 650 to 700 mm annum⁻¹, largely received during summer from November to February. The average minimum and maximum temperatures are 7°C and 27°C, respectively. The vegetation type at TNR is Rand Highveld Grassland found within the Mesic Highveld Grassland (MHG) bioregion with *Themeda triandra*, *Elionurus muticus*, and *Thristachya leucothrix* being the most common grasses (Mucina et al. 2006).

Sections of this grassland (Brown et al. 2022) classified as belonging to the *Eragrostis curvula*-*Seriphium plumosum* midslope plateau grassland is heavily encroached by *Seriphium plumosum*, with densities as high as 9500 plants ha⁻¹ being recorded (Graham et al. 2020). This shrub is 0.6 m tall, and its canopy may spread as wide as 1 m², imposing severe shading on understory grasses (Van Zyl and Avenant 2018). The TNR is characterised by sandy soils emerging from various geological formations including Quartzite of the

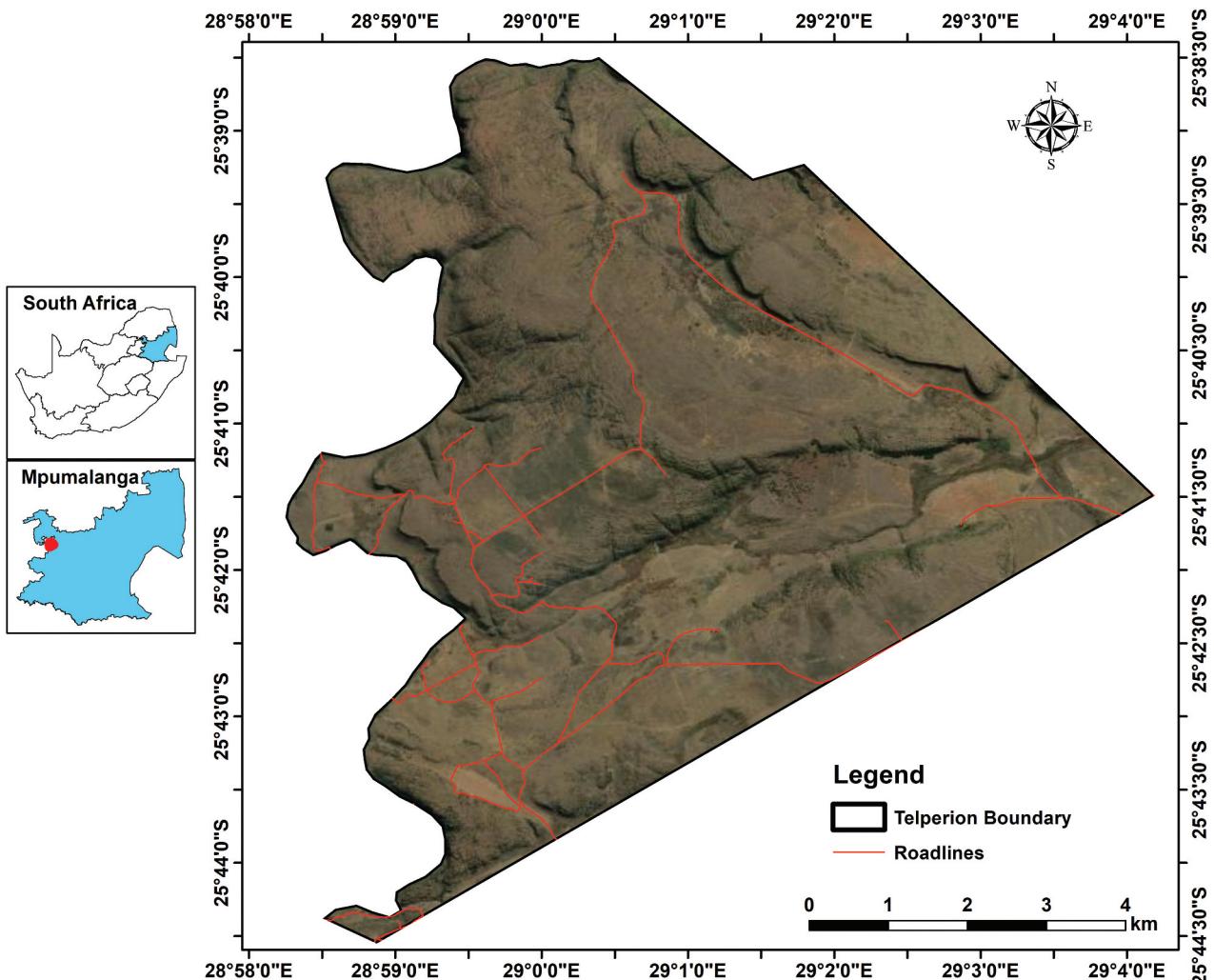


Figure 1. The study area, Telperion Nature Reserve, Mpumalanga Province, South Africa.

Witwatersrand Supergroup, Pretoria group and the Selons river formation of the Roiberg group (Mucina et al. 2006). The grassland is grazed continuously at a stocking rate of 0.20 large stock units by wild ungulates including black wildebeest (*Connochaetes gnou*), blue wildebeest (*Connochaetes taurinus*), blesbok (*Damaliscus pygargus*), red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*) and plains zebra (*Equus quagga*) (MacFadyen 2014). This reserve is used largely for the conservation of wild animal

biodiversity including small mammals, and large herbivores (MacFadyen 2014; Gumbi et al. 2018; Mndela et al. 2023a).

Experimental design

During the 2015 wet season, four $50\text{ m} \times 25\text{ m}$ blocks were demarcated randomly at four sites (Figure 2), under similar soil type, hydrology, and vegetation structure. These blocks were at least 1 km apart. Each block was divided into two paired $25\text{ m} \times 25\text{ m}$

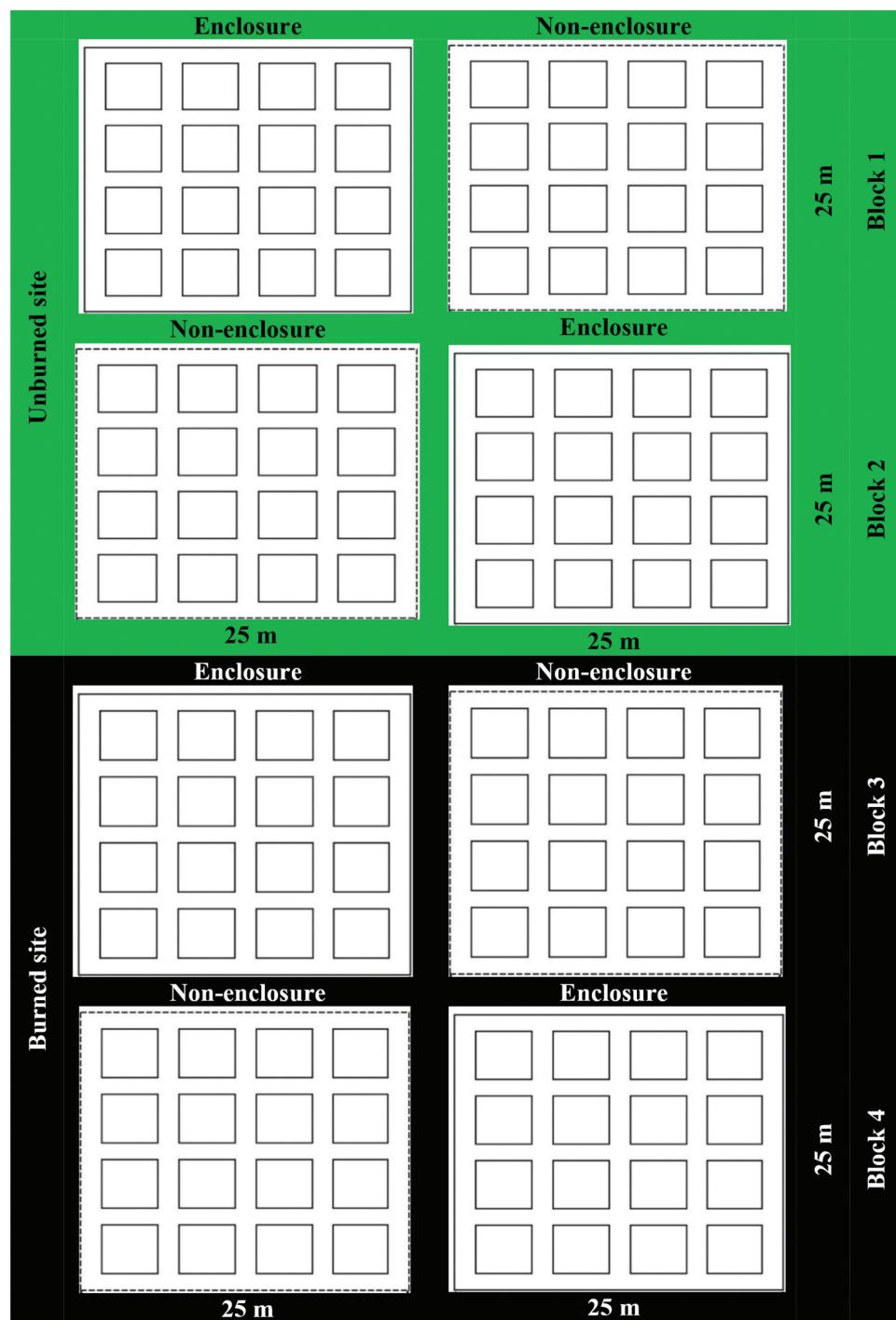


Figure 2. The layout showing the experimental design, Telperion Nature Reserve, Mpumalanga, South Africa. The $25\text{ m} \times 25\text{ m}$ plots are paired control enclosures and non-enclosures. The small plots inside are $4\text{ m} \times 4\text{ m}$ subplots nested within the enclosures and non-enclosed areas.

experimental plots, with one plot fenced to exclude herbivory (control – enclosures) and the adjacent one unfenced to permit herbivory (non-enclosures). Sixteen equidistant 4 m × 4 m observational units were nested within each enclosure and non-enclosure using permanent pegging with metal pins. Fires burned two blocks in 2020, leaving other two blocks unburned (Figure 2). This resulted in reconfiguring the experiment, thus having the following treatments: control untreated enclosures (-F-H), fire only (+F-H), herbivory only (-F+H) and fire combined with herbivory (+F+H) (Figure 2). Since 2020, these burned enclosures have been managed by applying controlled fires every two years. These experimental fires are applied to the direction of the wind after the first spring rains in August as hot head fires, with fire intensity ranging between 2001–3000 KJs⁻¹m⁻¹.

Data collection

A baseline data was collected in January 2015 before exclusion of wild ungulates in the control enclosures. The cover of vegetation including species of shrub, grass and forb species, plant densities, basal cover and species composition were assessed in thirty-two 4 m × 4 m subplots per block. Three 1-m² quadrats were sampled diagonally in two opposite corners and at the centre of each 4 × 4 m subplot. Post-treatment vegetation assessment was conducted late in the spring (late October) of 2022, seven years after establishment of the enclosure and herbivory experiment and two years after the wildfire. Herbaceous plants and shrubs were identified at species level and counted in each quadrat using the nomenclature by Van Oudtshoorn (1999) for grasses and Van der Walt (2009) for forbs, legumes, shrubs, and sedges. The minimum and maximum basal diameters (crown diameters in different directions) were measured for each plant rooted in each quadrat using a standard measuring ruler. For rhizomatous grasses and geoxyllic shrubs, we identified each above-ground shoot as an independent plant and measured the extension of every shoot independently if the shoots were ≥10 cm apart. Herbaceous, shrub and bare soil covers were estimated by two independent recorders in each subplot. Shrub cover comprises *Seriphium plumosum* only. The estimates from the values estimated by the two recorders were averaged for canopy cover value estimates.

Relative abundance was calculated to determine the relative contribution of each species to the total abundance of all species. Plants were categorised according to their life form (annual or perennial), ecological status (increaser I and II, decreaser and invader), grazing value (high, average, low), growth habit (creeper or bunch) and successional stage [pioneer (I), subclimax (II) and climax (III)]. A decreaser species is a species that dominates in well-managed rangeland

that is in good condition, whereas increaser I and II species dominate in under-grazed and overgrazed rangelands, respectively (Tainton 1981). However, in this study, the increaser II category was generalised to include species that increase with any other type of disturbance, e.g. fire. For all categories, we used a plant identification book by Van Oudtshoorn (1999) for southern African rangelands which clearly outlines the life form, ecological status, grazing value, growth habit and plant succession stage. The plants were identified during peak growth when their inflorescences were visible to ensure precise identification. For unidentifiable species, e.g., geoxyles and forbs, specimens were collected, pressed and sent to the herbarium of the Agricultural Research of South Africa. Plant densities were estimated as the number of individuals m⁻² and richness was calculated as the total number of species encountered in each 1-m² quadrat. Plant density was calculated for each plant functional group such as grasses, sedges and non-graminoids (forbs, ferns, shrubs, and rushes). Basal cover (BC) was calculated as a total ellipsoid area of all basal parts of plants per quadrat and expressed as a proportion of the area of a quadrat. The species diversity was calculated using the Shannon Wiener's diversity index (H') according to Magurran (2004):

$$H' = - \sum_{i=1}^S P_i \ln P_i(1)$$

Where S is the number of species in each quadrat and P_i is the relative abundance of species i .

Sørensen's similarity index was used to compare communities among treatments. The index was expressed according to Chao et al. (2006) as follows:

$$\text{Sørensen} = \frac{2C_{ij}}{B_i + B_j} (2)$$

C is the number of species common in i^{th} and j^{th} treatment and B is total number of species in i^{th} and j^{th} treatment, respectively.

Statistical analysis

A preliminary analysis of the baseline data indicated no pre-treatment differences ($p > 0.05$) in the response variables among replicate plots (Table S1–6). This suggested that post-treatment differences on response variables were due to treatments (Table S7–13). Normality and homoscedasticity of post-treatment data were assessed using Kolmogorov-Smirnov and Levene's tests, respectively, and visualised using Q-Q plots. Except for shrub cover and species diversity, all parameters including species richness and basal cover met both assumptions (Figure S1). We applied $\log_{10}(x + 1)$ transformation for species diversity and square-root transformation for shrub cover.

Thereafter, analysis of covariance (ANCOVA), with shrub cover added as a covariate, was conducted to assess treatment effects (fixed effects) on vegetation cover, species richness, diversity, and plant density. Since there is a treatment integrating both fire and herbivory (+F+H), we did not conduct interactions between fire and herbivory. The interactions were assessed between plant functional groups and treatments for plant density. Since our study design has low replication, we used mixed effects models, with the experimental plots added as random factors, whereas observational units were nested within the experimental plots. Significant differences between treatments were affirmed at $p < 0.05$ using the Tukey HSD post-hoc test. To simplify data interpretation, we report mean \pm SE. Transformed mean and SE for shrub cover and species diversity were back-transformed to the original scale. Regression models were generated to investigate the relationships between shrub cover and herbaceous canopy cover, basal cover, density, richness, and diversity. We used a hierarchical clustering to create a heatmap for separating vegetation clusters according to species affinity to fire and herbivory treatments. Euclidean distance measure was used to

assess similarity between vegetation clusters. All analyses were conducted using JASP software version 0.16.3.

Results

Relationship between shrub cover and herbaceous vegetation

Herbaceous canopy cover ($R^2 = 0.73$), basal cover ($R^2 = 0.29$) and plant density ($R^2 = 0.39$) declined linearly ($p < 0.001$) along an increasing gradient of shrub cover (Figure 3), with the former declining at higher rate of 0.56% per unit increase in shrub cover. Similarly, an increase in shrub cover was associated with a significant decline ($R^2 = 0.39$, $p < 0.001$) in herbaceous species diversity and richness (Figure 3).

The effect of fire and herbivory on species composition

A total of 49 species, distributed across 16 families were recorded, with 26 grass species (Poaceae) dominating, followed by 13 forb species and five shrub

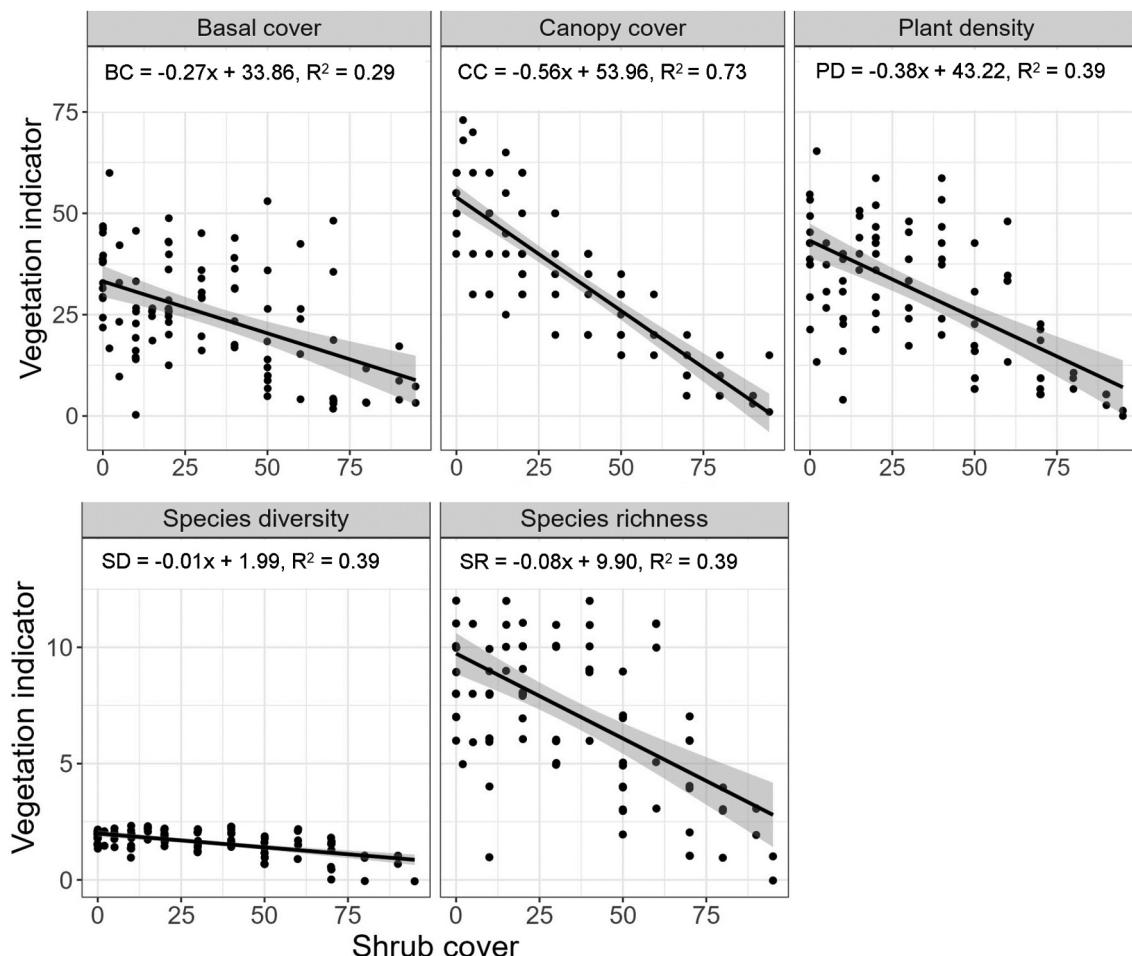


Figure 3. The relationships between shrub cover (%) and herbaceous plant species indicators (basal cover, canopy cover, species diversity, richness, and density) in a mesic grassland, Telperion Nature Reserve, South Africa. BC = basal cover, CC = canopy cover, PD = plant density, SD = species diversity and SR = species richness.

Table 1. Plant species composition across fire and herbivory treatments in the Telperion Nature Reserve, South Africa. L, lifespan; P, perennial; A, annual; ES, ecological status indicator; Incl, increaser I; incII, increaser II; inv, invader; SS, successional stage; I, pioneer; II, subclimax; III, climax; GF, growth form; -F-H, control (nor fire, no grazing); -F+H, no fire, herbivory; +F-H, fire, no herbivory; +F+H, fire and herbivory; GV, grazing value); H, high; A, average; L, low; N, no grazing value.

Species	Family	L ^Φ	ES [†]	GV	SS*	GF [‡]	Treatment			
							-F-H	-F+H	+F-H	+F+H
Grasses										
<i>Agrostis lachnantha</i>	Poaceae	P	Incl	A	III	Bunch	0.28	0.00	0.00	0.00
<i>Aristida congesta</i>	Poaceae	P	InclI	L	I	Bunch	5.29	4.55	1.16	4.20
<i>Aristida junciformis</i>	Poaceae	P	InclI	L	III	Bunch	0.00	0.00	0.00	3.47
<i>Aristida transvalensis</i>	Poaceae	P	Incl	L	III	Bunch	4.18	6.15	6.37	0.55
<i>Brachiaria serrata</i>	Poaceae	P	Dec	A	III	Bunch	0.00	0.00	0.00	0.91
<i>Cynodon dactylon</i>	Poaceae	P	InclI	H	I	Creeping	0.00	2.14	1.97	3.11
<i>Digitaria eriantha</i>	Poaceae	P	Dec	H	III	Bunch	1.39	1.87	3.48	6.58
<i>Elionurus muticus</i>	Poaceae	P	InclI	L	III	Bunch	0.00	0.00	2.90	3.84
<i>Enneapogon scoparius</i>	Poaceae	P	InclI	L	III	Bunch	1.95	0.00	0.23	0.00
<i>Eragrostis chloromelas</i>	Poaceae	P	InclI	A	III	Bunch	6.13	12.83	8.69	15.90
<i>Eragrostis curvula</i>	Poaceae	P	InclI	H	III	Bunch	5.29	6.42	10.54	13.16
<i>Eragrostis gumiiflua</i>	Poaceae	P	InclI	L	II	Bunch	0.00	5.61	0.81	5.30
<i>Eragrostis lehmanniana</i>	Poaceae	P	InclI	A	III	Bunch	0.00	0.00	0.93	0.00
<i>Harpochloa falfynx</i>	Poaceae	P	Incl	A	III	Bunch	0.00	0.00	2.78	5.48
<i>Heteropogon contortus</i>	Poaceae	P	InclI	H	II	Bunch	2.51	2.41	4.52	1.10
<i>Imperata cylindrica</i>	Poaceae	P	Incl	L	III	Creeping	16.43	3.48	0.00	0.00
<i>Leudetia simplex</i>	Poaceae	P	InclI	L	III	Bunch	0.00	0.00	0.23	0.00
<i>Melinis nerviglumis</i>	Poaceae	P	Incl	A	III	Bunch	0.00	0.00	0.81	0.00
<i>Melinis repens</i>	Poaceae	P	InclI	L	II	Bunch	1.95	8.29	6.95	2.38
<i>Perotis patens</i>	Poaceae	P	InclI	L	I	Bunch	0.56	7.22	4.17	2.19
<i>Pogonatheria squarosa</i>	Poaceae	P	InclI	L	III	Bunch	5.01	2.41	0.58	1.46
<i>Setaria sphacelata</i>	Poaceae	P	Dec	H	III	Bunch	13.93	23.53	7.07	1.83
<i>Schizachyrium sanguineum</i>	Poaceae	P	Incl	L	III	Bunch	1.11	0.27	0.70	0.00
<i>Themedia triandra</i>	Poaceae	P	Dec	H	III	Bunch	0.00	0.27	1.16	3.11
<i>Trachypyon spicatus</i>	Poaceae	P	Incl	L	III	Bunch	1.11	0.00	0.00	0.18
<i>Tristachya leucothrix</i>	Poaceae	P	Incl	A	III	Bunch	0.00	0.00	2.04	0.37
Total							67.13	87.43	67.74	75.14
Sedges										
<i>Cyperus</i> species	Cyperaceae	A	InclI		I	Bunch	3.90	1.07	0.46	0.91
<i>Fimbristylis hispidula</i>	Cyperaceae	A	InclI		I	Bunch	16.16	2.14	14.76	14.99
Total							20.06	3.21	15.22	15.90
Forbs										
<i>Achyranthes aspera</i>	Amaranthaceae	A	InclI		I	Bunch	0.56	0.00	0.12	0.00
<i>Cleome maculata</i>	Caparaceae	A	InclI		I	Bunch	0.56	0.53	1.16	0.00
<i>Commelina africana</i>	Commelinaceae	A	InclI		I	Bunch	0.00	0.00	1.51	0.55
<i>Gomphrena serrata</i>	Amaranthaceae	A	InclI		I	Creeping	0.84	1.34	0.00	0.18
Forb species	-	A	InclI		I	Bunch	1.67	0.00	0.58	0.00
<i>Helichrysum rigidulum</i>	Asteraceae		InclI		I	Bunch	0.00	1.34	0.23	0.00
<i>Justicia anagalloides</i>	Acanthaceae	P	InclI		I	Bunch	0.00	0.00	0.12	0.00
<i>Monsonia angustifolia</i>	Geranaceae	A	InclI		I	Bunch	0.56	0.00	0.81	0.00
<i>Oxalis latifolia</i>	Oxalidaceae	A	InclI		I	Creeping	0.28	0.00	0.00	0.00
<i>Phyllanthus parvulus</i>	Euphorbiaceae	A	InclI		I	Bunch	2.79	2.41	1.27	1.46
<i>Tephrosia lupinifolia</i>	Fabaceae	P	InclI		I	Bunch	0.00	0.27	0.12	0.00
<i>Vernonia poskeana</i>	Asteraceae	A	InclI		I	Bunch	0.00	0.00	1.97	0.00
Total							7.24	6.15	9.62	2.19
Shrubs										
<i>Elephantorrhiza elephantina</i>	Fabaceae	P	InclI			Geoxyle	0.00	1.34	1.62	0.18
<i>Fadogia homblei</i>	Rubiaceae	P	InclI			Geoxyle	0.56	0.00	0.70	0.73
<i>Parinari capensis</i>	Chrysobalanaceae	P	InclI			Geoxyle	0.00	0.00	3.01	5.48
<i>Salacia rehmanii</i>	Celastraceae	P	InclI			Geoxyle	0.00	0.00	1.62	0.00
Tephrosia species	Fabaceae	P	InclI			Bunch	0.56	0.00	0.00	0.18
Total							1.11	1.34	6.95	6.58
Others										
<i>Hypoxis rigidula</i>	Hypoxidaceae	P				Bunch	4.46	0.53	0.00	0.00
<i>Nephrolepis cordifolia</i>	Nephrolepidaceae	P				Bunch	0.00	1.34	0.12	0.00
Succulent species	Euphorbiaceae					Bunch	0.00	0.00	0.35	0.18
Total							4.46	1.87	0.46	0.18

species (Table 1). Grass abundance was higher in the -F+H treatment (87.4%) relative to +F-H (67.7%) and +F+H (75.1%) and the control (-F-H), with *Setaria sphacelata* dominating by 24% (Table 1). *Eragrostis chloromelas*, *E. curvula* and *Fimbristylis hispidula* co-dominated in the +F-H and F+H treatments, having covers of 8.7 and 15.9%, 10.5 and 13.2%, and 14.7 and 15.0%, respectively (Table 1).

Cluster analysis of species abundance data separated four distinct vegetation clusters (Figure 4). Cluster 1 (C1), the largest and most species-rich vegetation unit was associated with the +F-H treatment (Figure 4). It was characterised by geoxyllic shrubs (*Elephantorrhiza elephantina* and *Salacia rehmanii*), climax grasses (*Tristachya leucothrix*, *Aristida transvalensis*, *Melinis nerviglumis*, *Loudetia simplex* and *Eragrostis lehmanniana*)

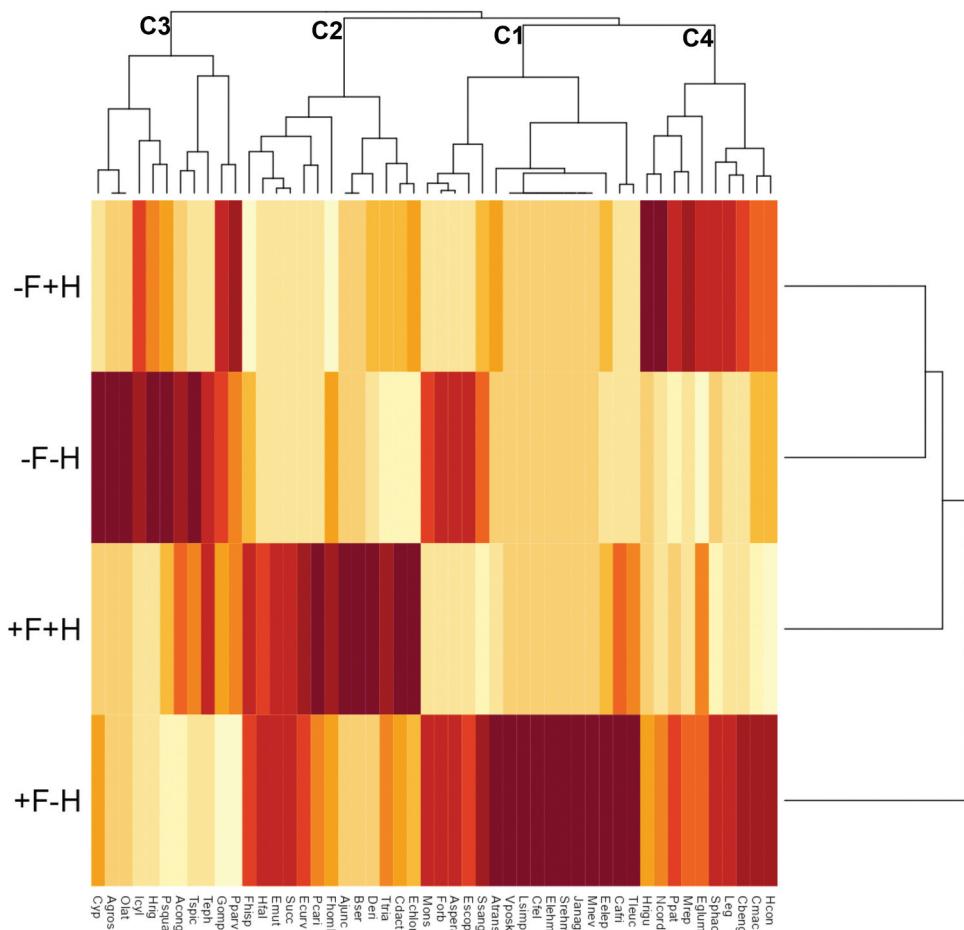


Figure 4. A heatmap separating vegetation clusters across fire and herbivory treatments in a mesicgrassland of Mpumalanga. C1, 2, 3 and 4 are vegetation clusters. Key to treatments: +F+H; fire by herbivory combination, +F-H; fire only, -F+H; herbivory only, -F-H; untreated enclosures. The stronger the colour the higher the abundance in each treatment. Key to species: Hcon = *Heteropogon contortus*, Cmac = *Cleome maculatae*, Cbeng = *Commelina benghalensis*, Leg = *Tephrosia lupinifolia*, Sphace = *Setaria sphacelata*, Eglum = *Eragrostis glumiflua*, Mrep = *Melinis repens*, Ppat = *Perotis patens*, Ncord = *Nephrolepis cordifolia*, Hrigu = *Helichrysum rigidulum*, Tleauc = *Trastichya leucothrix*, Cafri = *Commelina africana*, Eelep = *Elephantorrhiza elephantina*, Mnev = *Melinis nerviglumis*, Janag = *Justicia anagalloides*, Srehm = *Salacia rehmanii*, Elehm = *Eragrostis lehmanniana*, Lsimp = *Loudetia simplex*, Vposk = *Vernonia poskeana*, Atrans = *Aristida transvaalensis*, Ssang = *Schizachyrium sanguinum*, Escop = *Enneapogon scoparius*, Aspera = *Achyranthes aspera*, Forb = unknown forb, Mons = *Monsonia angustifolia*, Echboro = *Eragrostis chloromelas*, Cdact = *Cynodon dactylon*, Ttria = *Themeda triandra*, Deri = *Digitaria eriantha*, Bser = *Brachiaria serrata*, Ajunc = *Aristida junciformis*, Fhomb = *Fadogia homblei*, Pcar = *Parinari capensis*, Ecurv = *Eragrostis curvula*, Succ = Unidentified succulent, Emut = *Elionurus muticus*, Hfhal = *Harpochloa falfynx*, Fhisip = *Fimbristylis hispidula*, Pparv = *Phyllanthus parvulus*, Gomp = *Gomphrena serrata*, Teph = *Tephrosia* species, Tspic = *Trachypogon spicatus*, Acong = *Aristida congesta*, Psqua = *Polygonathria squarosa*, Hrig = *Hypoxis rigidula*, Icyl = *Imperata cylindrica*, Olat = *Oxalis latifolia*, Agros = *Agrostis lachnantha*, Cyp = *Cyperus* species.

and some forbs (Figure 4). Similarly, C2 was characterised mainly by climax grass species ($n = 10$) and some geoxyllic shrubs ($n = 2$) and was associated largely with the +F-H treatment. This cluster was dominated by *Eragrostis curvula*, *E. chloromelas* and *Fimbristylis hispidula* (Table 1; Figure 4). C3 was characterised by disturbance intolerant or increaser I species, mostly recorded in the control (-F-H), with *Imperata cylindrica* being the dominant species (Table 1; Figure 4). C4 had a low species richness and was associated with both +F-H and -F+H treatments (Figure 4). There was low similarity in species composition between control and +F-H ($\text{Sørensen} = 0.59$) and control and the +F+H treatment ($\text{Sørensen} = 0.57$; Table 2). Conversely, the

vegetation clusters of +F-H and +F+H treatments were similar ($\text{Sørensen} = 0.69$) and they were similar to that of the -F+H treatment ($\text{Sørensen} = 0.65\text{--}0.69$; Table 2).

Table 2. Sørensen's similarity index indicating plant community similarity among control, fire and herbivory treatments, Telperion Nature Reserve, South Africa. -F-H, control; -F+H, herbivory only; +F-H, fire only; +F+H, fire and herbivory treatment.

	-F-H	-F+H	+F-H	+F+H
-F-H	*	0.68	0.59	0.57
-F+H		*	0.69	0.65
+F-H			*	0.69
+F+H				*

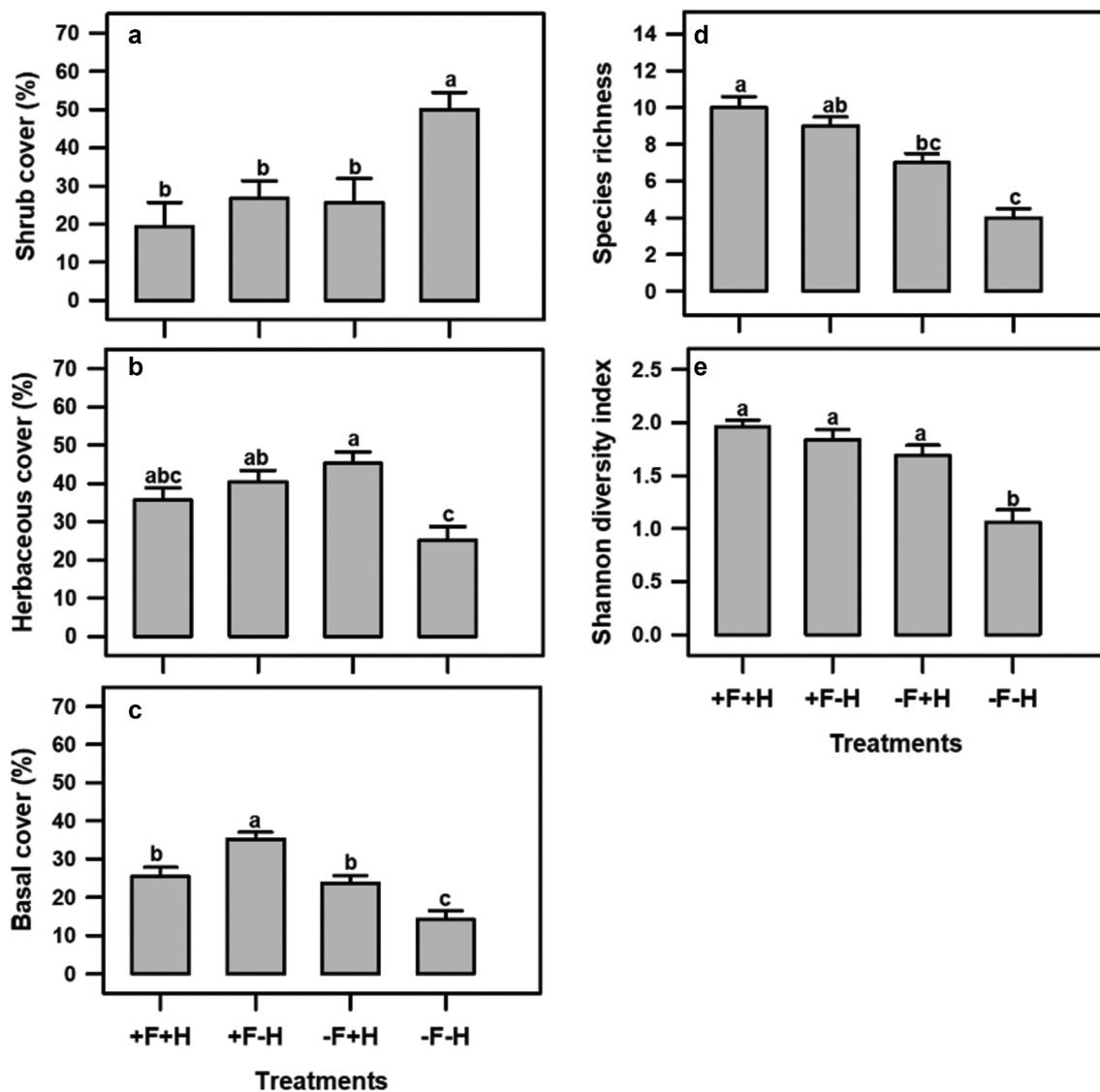


Figure 5. Vegetation cover (A, B, C), richness (D) and diversity (E) in fire and herbivory treatments. Whiskers represent standard errors. Different letters between bars indicate significant differences ($p < 0.05$) between means across treatments. Key to treatments: +F+H; fire by herbivory combination, +F-H; fire only, -F+H; herbivory only, -F-H; untreated enclosures.

Vegetation cover

The treatments had a significant effect on the cover of shrubs ($F_{3, 92} = 7.51, p < 0.001$) and herbaceous species ($F_{3, 92} = 6.80, p < 0.001$) as well as on basal cover ($F_{3, 92} = 21.76, p < 0.001$; Figure 5A–C). The control (-F-H) had two to three-fold more shrubs cover than either of the treatments (Figure 5A). Herbaceous species cover was higher in the +F-H ($p = 0.002$) and -F+H treatments ($p < 0.001$) than in the control (Figure 5B). Basal cover was higher in the +F-H treatment than in the -F+H treatment ($p = 0.007$) or in the +F+H treatment ($p = 0.027$) and it was double compared to that in the control ($p = 0.008$; Figure 5C).

Species richness and diversity

All treatments had significantly greater species richness ($F_{3, 92} = 21.76, p < 0.001$) and diversity ($F_{3, 92} =$

21.76, $p < 0.001$) than the control (Figure 5D – E). Species richness was comparable between the +F-H and +F+H treatments ($p = 0.352$), with both treatments having two to three times more species than the control (Figure 5D). The +F+H treatment had more species ($p = 0.021$) than the -F+H treatment. The species diversity in the treatments was similar ($p > 0.05$) and was higher than in the control ($p < 0.001$; Figure 5E).

Plant density

Total plant density was significantly increased in the treatments ($F_{3, 92} = 22.56, p < 0.001$). It was highest in the +F+H treatment (46 ± 4 plants m^{-2}), followed by +F-H (36 ± 2), -F+H (31 ± 3) and lowest in the control (17 ± 2) (Figure 6). Plant density was affected by the interaction between treatment and plant functional groups ($F_{6, 276} = 14.17, p < 0.001$). Grasses attained,

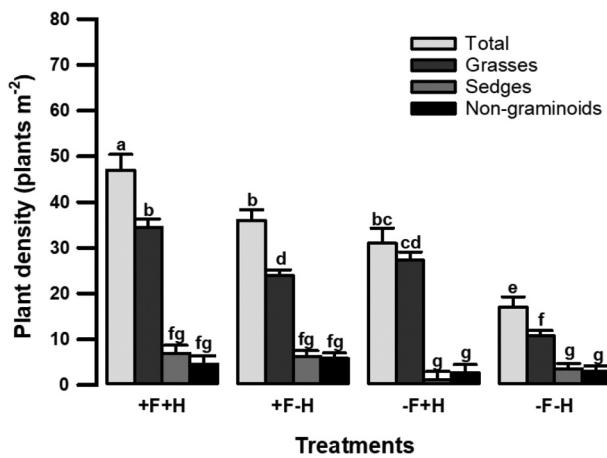


Figure 6. Densities of different plant functional groups in fire and herbivory treatments in mesic grassland of Mpumalanga. Different letters between bars indicate significant differences ($p < 0.05$) between means across treatments. Key to treatments: +F+H; fire and herbivory combination, +F-H; fire only, -F+H; herbivory only, -F-H; untreated enclosures.

on average, 4 to 15-fold higher densities compared to other plant functional groups in the treatments (Figure 6). Grass densities were higher in the +F+H treatment than in the +F-H and control ($p < 0.001$) but did not differ from that in the -F+H treatment ($p = 0.143$; Figure 6).

Discussion

Effect of shrub encroachment on herbaceous vegetation

Our results revealed that an increase in *Seriphium plumosum* shrub cover reduces herbaceous plant cover, species richness and diversity in this South African mesic grassland. Our findings thus disagree with those by Graham et al. (2020) who found that some degree of *S. plumosum* encroachment enhanced herbaceous vegetation diversity, species richness and productivity. According to our results, early control of this shrub is necessary to avoid negative changes in ecosystem structure that can reduce potential ecosystem services. *Seriphium plumosum* forms a dense canopy that limits access to light and has vigorous root system enabling high soil nutrient and moisture uptake at the expense of understorey grasses (Van Zyl and Avenant 2018). The decline in herbaceous cover could be ascribed to poor vegetative performance, e.g. reduced leaf production and leaf area index due to shading (Irving 2015). Canopy shading by shrubs induces premature leaf senescence and depletes tiller production, resulting in low leaf production of understorey grasses (Mndela et al. 2022b).

The fact that herbaceous plant cover was positively related to plant density and species richness suggests that a decline in these vegetation attributes

was responsible for the decline in herbaceous cover and diversity (Figure S2). The decline in density and loss of species together with decline in basal cover leave the soil surface unprotected from direct rain splash, resulting in water erosion and soil loss. Similarly, other studies such as Casado et al. (2004) and Boscutti et al. (2018) have found negative linear relationship between species richness and shrub cover. Generally, the competition for resources between shrub and herbaceous species is negligible at low shrub cover and the conditions are suitable for shade-intolerant species, but as encroachment increases, some species disappear (Graham et al. 2020). However, in this study, we found linear declining relationships, indicating that the encroacher poses immediate negative effects on herbaceous species diversity, density, and richness. These effects are not only a function of competition, but also of allelopathic effects imposed by the shrub, causing plant mortality and reduction in understorey recruitment and establishment (Snyman 2010; Van Zyl and Avenant 2018).

Using segmented regression to determine break points as proxies for shrub cover threshold, we found zero break points for all parameters, highlighting that even at low shrub cover, *S. plumosum* has detrimental effects on herbaceous species.

The effect of fire and herbivory on herbaceous species composition

The dominance of climax grasses indicates that the vegetation of this mesic grassland is stable despite the fire and herbivory disturbances, and this appears to be driven by the occurrence of species adapted to these disturbances. For example, the fire only and fire plus herbivory treatments were dominated by fire-tolerant *Eragrostis* species (Phillips 2012) and geoxyllic shrubs (Maurin et al. 2014). As a result, the plant species composition in these treatments was very similar, indicating that fire was the main disturbance factor that governed the occurrence of species. In fact, dominance of *Eragrostis* species and *Fimbristylis hispidula* in the fire with herbivory treatment is an indicator of a grassland subjected to intense fires and heavy grazing (Phillips 2012; Masunga et al. 2013). This was also affirmed by high richness of increaser II grass species which generally thrive under frequent burning and heavy grazing (Van Oudtshoorn 1999). Furthermore, the occurrence of geoxyles, although at low abundance, in the treatments with fire indicated that fire also encourages the occurrence of species with well-protected below-ground structures. For example, *Elephantorrhiza elephantina*, *Fadogia homblei* and *Parinari capensis* resprout successfully from their geoxyllic suffrutices owing to their high below-ground carbohydrates storage and insulation of their



meristems by soil from fires and herbivory (Maurin et al. 2014). However, dominance of bunch grasses relative to creeping species disagrees with findings from other studies (e.g. Archibald 2008), that pyric herbivory favours short-statured creeping lawns. Our observations agree with many other studies that have assessed fire effects in other South African mesic grasslands (e.g. Buthelezi et al. 2016). Nonetheless, the composition of the herbivory only treatment to some degree resembled that of fire only and fire combined with herbivory treatments. This was driven by the occurrence of disturbance tolerant species in both the herbivory and fire treatments.

Fire and herbivory reduce shrub cover and restore herbaceous vegetation

Fire and herbivory either singularly, or in combination, effectively reduced the cover of *S. plumosum*. However, the results by Clark et al. (2020) on herbivory effects on *S. plumosum* cover disagree with our findings. The disagreement between our results and those by Clark et al. (2020) could be due to differences in animal types and grazing systems applied in the two studies. Even though cattle graze *S. plumosum* seedlings and its post-fire regrowth (Du Toit 2012), the period of cattle absence in the encroached paddocks during rotational grazing, probably allowed shrub recovery in the study by Clark et al. (2020). Furthermore, wild ungulates browse more efficiently than cattle, effectively breaking the twigs of shrubs, thereby reducing shrub cover (Riginos and Young 2007).

Although *S. plumosum* is capable of resprouting following disturbance (Snyman 2005), it appears that fire combined with herbivory is an effective means to control it (Werner et al. 2021). The fire combined with herbivory treatment operates as a leader-follower system, with resprouts of partially burned shrubs being suppressed by wild ungulates via trampling and browsing (O'Connor et al. 2020). In this study, regardless of the type of disturbance, all treatments increased herbaceous plant cover. Fire and herbivory, through reducing shrub cover, facilitated the recruitment of herbaceous species and their establishment, as indicated by increased plant densities and cover. These disturbances increase light, soil moisture and nutrient availability in herbaceous plants (Venter et al. 2017; O'Connor et al. 2020). Thus, increased herbaceous plant cover and densities suggests that fire and herbivory are essential disturbances for maintaining mesic grassland structure.

While fire and herbivory treatments, independently, had significant effects on plant densities, their combination had enhanced effects, especially so on grass densities. This could be ascribed to the increased abundance of grazing and fire tolerant grass species,

e.g. *Eragrostis chloromelas* and *E. curvula*. These species are obligate seeders and their seedling recruitment is enhanced by fire (Snyman 2005), whereas adult plants recover vigorously via increased tiller turnover following fires (MacFarland and Mitchell 2000). As fire occurred during the dry season at Telperion when the plants were dormant and already translocated carbohydrates to their roots, plants are likely to have resprouted using below-ground stored reserves (Venter et al. 2017; Simpson et al. 2021). In accordance with our results, Snyman (2005) has reported a two-fold increase in abundance of *E. chloromelas* after fire compared to pre-fire. A significant interaction between treatment and plant functional groups on plant densities suggests that grasses, forbs, and sedges exhibit differential responses to fire and wild ungulates. Some grass species have co-evolved with grazing and fire disturbances (Phillips 2012); hence they are more resilient to these selective pressures than other functional groups. Moreover, since some grass species have low palatability, they are avoided by grazing ungulates (Venter et al. 2017), which probably protects their seed production and increases their contribution to recruitment.

Species richness was higher in the treatment where fire was combined with herbivory compared to the treatment with herbivory only and was comparable to that in the fire only treatment, suggesting that fire is more effective in enhancing species heterogeneity than herbivory. This is surprising, given that herbivory through trampling, grazing, and excretion facilitates habitat heterogeneity (Marion et al. 2010). The higher species richness in the fire treatments was related to an increase in fire tolerant species including geoxyllic shrubs which did not occur in the herbivory treatment or in the control. However, similar species diversity across the three treatments indicates that diversity depends not only on species numbers, but also on the abundance of individual species. Thus, where species over-dominance is limited, diversity increases.

Implications for management, biodiversity conservation and wild ungulate grazing

The relationships between the cover of shrub and herbaceous plant species are a basis to developing appropriate management plans in ecosystems prone to shrub encroachment. As in other studies (e.g. Roques et al. 2001; Zehnder et al. 2020), our results revealed that shrub encroachment reduces herbaceous cover, density, diversity, richness, and basal cover. Although shrub management strategies have been recommended for *S. plumosum* control (e.g. Marquart et al. 2022), in this study we assessed the most cost-effective measures which have long co-evolved with grassland ecosystems (Clark et al. 2020).

While all treatments investigated in this study led to improvement, fire combined with herbivory was the best treatment to reduce shrub cover and to increase plant density, diversity, and richness. However, this treatment was dominated by increaser II species whose abundance increases with heavy grazing and these species are undesirable for grazing (Tainton 1981). This finding indicates that wild ungulates exert an intense grazing pressure following fires and this calls for a prescribed grazing and fire regime that will drive species composition to the dominance of decreaser grass species. Amongst other strategies, multiple patch burning is suggested to encourage the spread of wild ungulates across the landscape following fires. Manipulating the spatial distribution of ungulates through patch burning reduces patch selectivity and minimises grazing pressure on frequently visited burned areas (Smit et al. 2016). This strategy also facilitates landscape heterogeneity (Fuhlendorf et al. 2008) and promotes variation in nutritional quality of grasses to meet animal species-specific nutritional requirements (Weir et al. 2013). The practicality and efficacy of this management strategy, however, needs to be tested in the mesic grasslands of South Africa. Future research is recommended to determine how spot burning affects animal distribution and how such effects shape vegetation composition, structure and productivity.

Conclusions

Seriphium plumosum causes ecosystem deterioration via negative effects on herbaceous plant species, thus calling for shrub control. All shrub control methods in this study effectively reduced *S. plumosum* cover and improved herbaceous plant species cover, diversity, and density, showing that these disturbances are key for the maintenance of mesic grassland structure and composition. Integration of fire and herbivory into management strategies of mesic grasslands holds greater promise than when applied alone for plant species conservation and grassland restoration purposes. The findings of this study are key to policy making and local management of mesic grasslands. These include designing a shrub control framework including prescribed fire management and grazing programmes to combat *S. plumosum* encroachment at the landscape scale. However, while the results of this study are promising, the appropriate burning frequency and season to effectively combat shrub encroachment are yet to be evaluated. Thus, long-term monitoring and identification of appropriate fire frequency that may successfully combat encroachment and optimise herbaceous vegetation recovery is necessary.

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ORCID

Mthunzi Mndela  <http://orcid.org/0000-0002-2384-6856>
Alan S. Barrett  <http://orcid.org/0000-0001-8433-6828>
Leslie R. Brown  <http://orcid.org/0000-0002-1026-5438>

Author contributions

MM, AB and LRB conceived the idea and designed the research. MM performed data collection, curation, and analysis. MM wrote the manuscript. AB, MKS and LRB read several drafts of the manuscript and provided valuable comments and corrections. All authors agree on the submission of the manuscript for publication.

Data availability statement

The data used in this study will be made available on request.

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