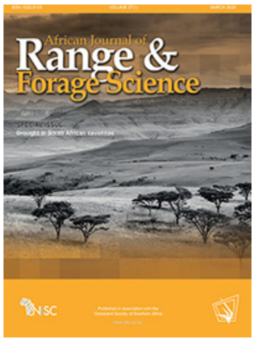

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Forb community responses to an extensive drought in two contrasting land-use types of a semi-arid Lowveld savanna

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Projected increases in the frequency and severity of drought events are expected to impose changes in the ecology of native forb communities in semi-arid ecosystems. We examined the state of forb communities during, and directly after an extreme drought event across two contrasting land-use types, which included a protected area (high diversity of free roaming wild herbivores) and communal rangeland (long history of intensive cattle grazing) in a semi-arid Lowveld savanna of the Gazankulu area, South Africa. Forb floristic data were collected towards the end of the drought and repeated after the drought release a few months later. Forb community composition was significantly different among land-use types. Community changes were not induced by annual forb emergence alone, but through species-specific dominance shifts, which differed among land-use types. Forb richness, diversity and biomass were equally low at both land-use types and increased significantly after the drought release, although the magnitude of response was much stronger in the protected area, whereas drought contributed to a directional change in the protected area with a complete post-drought turnover in both annual and perennial forb species, much less variability was observed in the communal rangeland, which may suggest long-term effects imposed by land-use history.

Keywords: climate change, diversity, grazing, herbivory, rainfall variability

Introduction

Ecological research in semi-arid savannas is increasingly focused on quantifying ecosystem responses to global environmental change (Ruppert et al. 2015; Bunting et al. 2018). Biodiversity and the maintenance of terrestrial ecosystem functioning are threatened by climate change (Midgley and Bond 2015; Van Wilgen et al. 2016) combined with non-sustainable land-use practices (Newbold et al. 2015). In African savannas, changes in the assembly and density of herbivores, especially increasing livestock densities at the cost of a diverse suite of native herbivores with whom these ecosystems evolved, combined with predictions of future increases in drought events are of particular concern (Ruppert et al. 2015; Zerbo et al. 2016; Riginos et al. 2018). Quantifying such land-use and climate effects on savanna herbaceous vegetation dynamics is essential for the management and conservation of semi-arid ecosystems, because herbaceous plants provide important goods and services to African livelihoods (Martin et al. 2016).

Studies on herbaceous vegetation dynamics are strongly focused on grass productivity related to grazing and climate variability (Trollope et al. 2014) with limited focus on forbs (non-graminoid herbaceous vascular plants) (Siebert and Dreber 2019). Forbs are an important source of biodiversity in grasslands and savannas (Uys 2006; Buitenwerf et al. 2011; Trollope et al. 2014; Scott-Shaw and Morris 2015; Siebert and Scogings 2015) that are functionally diverse, which suggest stronger resilience to environmental disturbances (Shackleton 2000; Jacobs and Naiman 2008; Bond and Parr 2010; Scott-Shaw and Morris 2015; Van Coller et al. 2018). Furthermore, forbs provide nutritious forage resources across herbivore guilds, from insects (Andersen and Lonsdale 1990) to wild native herbivores and cattle (Odadi et al. 2007). Cattle may even suppress forb cover through forb forage preferences towards the end of a dry season (Young et al. 2005; Odadi et al. 2007; Kimuyu et al. 2017). Despite significant contributions to ecosystem goods and services, both annual and perennial forbs are often perceived negatively by land managers, because of their association with savanna land degradation (Siebert and Dreber 2019) and dominance over grasses under particular environmental conditions, such as on nutrient-rich soils (Reich et al. 2003; Van Coller and Siebert 2015), when grazing pressure is moderate to high (Scholes 1987; Hejcmanová et al. 2010; Cowley et al. 2014) or after drought events (Fynn and O'Connor 2000; Buitenwerf et al. 2011).

The majority of studies that are aimed at describing grazing and/or drought impacts in savanna ecosystems are not particularly designed for an improved understanding of forb community ecology, neither the drivers responsible for community dynamics (Siebert and Dreber 2019). Nevertheless, some notes on forb dynamics in rangeland studies are useful contributions to our current understanding. For instance, similar to what is known for grasses, herbivory, climate (particularly rainfall variability), fire and microhabitat properties are considered as important drivers of forb community dynamics in semi-arid and arid savannas (Siebert and Dreber 2019).

Forb community responses to herbivory are unpredictable, because it largely depends upon herbivore type (Odadi et al. 2017), grazing intensity (Dreber et al. 2011; Rutherford et al. 2012; Hanke et al. 2014; Linstädter et al. 2014), duration (Tessema et al. 2011; Odadi et al. 2017) and seasonality (Angassa and Oba 2010). For instance, long-term high intensity livestock grazing in savanna ecosystems may result in community shifts in favour of grazing resistant or –tolerant forbs (Dreber et al. 2011; Hanke et al. 2014; Tessema et al. 2016), as a result of significant changes in soil properties (Metzger et al. 2005; Tessema et al. 2011), seed banks (Dreber et al. 2011) and tree-grass balances (Angassa 2012). Changes in the type of herbivore guild grazing may induce long-term changes in forb communities (Odadi et al. 2017), although the direction of change may differ across ecosystem and herbivore types. High grazing pressure from cattle and goats on communal rangelands in an arid South African savanna have shown negligible effects on the overall forb community, although increased abundances of some perennial forbs were reported (Linstädter et al. 2014). In contrast, a significant reduction in perennial forbs and increases in annual, prostrate forbs under high communal grazing pressure by goats was reported in an arid Nama-Karoo savanna ecosystem (Dreber et al. 2011; Hanke et al. 2014). In areas where diverse assemblages of herbivores are being protected, grazing impacts are less defined, although exclusion of herbivores from such ecosystems have been reported to have significant effects on forb communities (Jacobs and Naiman 2008; Young et al. 2013; Van Coller et al. 2018). Long-term exclusion of wild ungulate grazing and browsing from a nutrient-rich sodic savanna in South Africa resulted in declines in forb species richness. When overtopped by tufted perennial grasses in the absence of large mammals, perennial forbs may persist, although annual forb abundances are dependent upon disturbance-induced and nutrient-enriched open areas (Van Coller et al. 2018). Declining numbers of wildlife and subsequent increases in livestock density have also revealed herbaceous community shifts towards a reduction in forb abundances (Young et al. 2013).

Forb community assemblages, structure and diversity are furthermore shaped by interannual rainfall variability (Clegg and O'Connor 2017; Zerbo et al. 2018), although they seem to be less sensitive than grasses to periodic droughts (O'Connor 1998; Fynn and O'Connor 2000). Semi-arid savanna forbs are particularly rich in functional traits (Hanke et al. 2014; Van Coller and Siebert 2019), which make them resilient to environmental fluctuations. Forbs have a strong ability to persist during droughts, largely as a result of decreased competition with tufted perennial grasses, which are often depleted after an extensive drought (O'Connor 1998). After drought events, forbs emerge before grasses and often dominate the herbaceous layer while the grasses recover (Fynn and O'Connor 2000; Kallah et al. 2000; Buitenwerf et al. 2011). Drought events in grassland ecosystems may increase native annual forbs in the seed bank (LaForgia et al. 2018), although emergence following disturbances may be species-specific for forbs (Siebert and Dreber 2019).

Despite available knowledge on how forbs (as a life form) respond to common drivers of herbaceous dynamics, our understanding of the effects of such disturbances (e.g. herbivory) combined with rainfall variability (e.g. drought events) on forb species composition and diversity, is limited. This study therefore sought to quantify the status of forb communities during, and directly after a severe drought event in a semi-arid Lowveld savanna of South Africa under two contrasting land-use types within a similar vegetation type and climate bioregion. Land-use types included a (i) communal rangeland and (ii) protected area.

Traditional communal rangelands in South Africa are often perceived as degraded landscapes that are unsustainable and unproductive (Shackleton 1993) and yet, they often host more plant species, most of which include forbs, than the neighbouring protected areas (Shackleton 2000). Under moderate to high grazing pressure, drought may induce compositional shifts in the herbaceous layer from a perennial grass-dominated state to an alternate state characterised by unpalatable, weakly tufted perennial grasses and annual forbs (Fynn and O'Connor 2000; Morecroft et al. 2004; Vetter 2009; Porensky et al. 2013; O'Connor 2015). We therefore expected a shift in forb community composition driven by post drought dominance of annual forbs in the communal rangeland land-use type. Furthermore, because communal cattle often depend on forb forage during dry periods when other food resources are limited, we expected forb communities to be depleted by overgrazing towards the end of the severe drought event, and the forb species that persisted being grazing- and drought-tolerant perennials. Private game reserves in the Lowveld of South Africa function as protected areas with the mandate of conserving biodiversity (Shackelton 2000). Considering that the diverse community of native herbivores in the protected area depends on various food resources, dispersing the pressure on foraged vegetation (Fynn 2012; Kartzinel et al. 2015), it was expected that forb communities that persisted during the drought would be dominated by drought-tolerant perennials and few, if any, annual species. Responses to the release of the extensive drought event a few months later, were expected to induce significant changes in forb communities (Fynn and O'Connor 2000; Zerbo et al. 2016), with community composition, richness, diversity and productivity being divergent among the contrasting land-use types, as a result of different land uses and hence, disturbance histories. Post-drought dominance of annual forbs in disturbed ecosystems (O'Connor 1998; Bat-Oyun et al. 2016) led us to predict weak responses to the drought release with regards to forb evenness and hence diversity in the communal rangeland (Hillebrand et al. 2008). However, the taxonomic and functional diversity of forbs (Bond and Parr 2010) led us to predict that forb responses to rainfall variability and land-use change would be species- and land-use type specific.

In this paper, we discuss the observed changes in forb community composition and diversity with a specific focus on dominance shifts between perennial and annual forbs (i.e. life-history trait dominance shift) and species-specific dynamics at each respective land-use type for an improved understanding of forb community responses to drought under different management systems.

Materials and Methods

Study site and experimental design

The two selected land-use types are located in the semi-arid Lowveld savanna of the Gazankulu area along the Klaserie–Orpen road (R531) in Mpumalanga, South Africa (Figure 1).

The Birmingham section of the Timbavati Private Nature Reserve (TPNR) (24°34′04″ S, 31°19′11″ E) represented the protected area land-use type, which hosts a diversity of indigenous wildlife since the 1970s, including mixed feeders, such as elephants (*Loxodonta africana*), impala (*Aepyceros melampus*) and steenbok (*Raphicerus campestris*), browsers, such as greater kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*) and bushbuck (*Tragelaphus sylvaticus*), and grazers, such as Cape buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*) (Hirst 1975; Van der Waal et al. 2011). Management of private game ranches and reserves, such as TPNR prescribes lower stocking rates for protected areas (Peel et al. 2005; Matsika et al. 2013), although free animal movement across bordering reserves and the Kruger National Park may lead to dynamic stocking rates in private nature reserves. Water provision in the reserves attracted high numbers of herbivores during the drought (2015–2016), during which the stocking rate at the Birmingham section peaked at ~0.12 livestock units (LSU's) per ha, after which animal numbers stabilised at ~0.06 LSU's in 2017, when rainfall returned to normal (Data obtained from TPNR management).

The rural village of Welverdiend (24°34′15″ S, 31°20′42″ E) represented the communal rangeland land-use type, where herbivores are limited to domestic cattle and goats (Shackleton 2000; Matsika et al. 2013). Livestock grazing at Welverdiend dates back between 1930 and 1940 (George 2000) and increased in intensity as human population increased in the area (Shackleton 2000). Stocking rates are well above the ecological carrying capacity of 0.88 (± 0.09) livestock units (LSU) per ha (Parsons et al. 1997) and peaked at >1.0 LSU ha^{-1} in 2016.

The landscape has a flat to undulating topography, giving rise to a catenal sequence that includes a complete series of terrain morphologies (Kaschula et al. 2005). On a national scale the study site is located within the Granite Lowveld vegetation unit (SVI 3) of the Savanna Biome (Mucina and Rutherford 2006). Crests, in which vegetation surveys were undertaken for the purpose of this

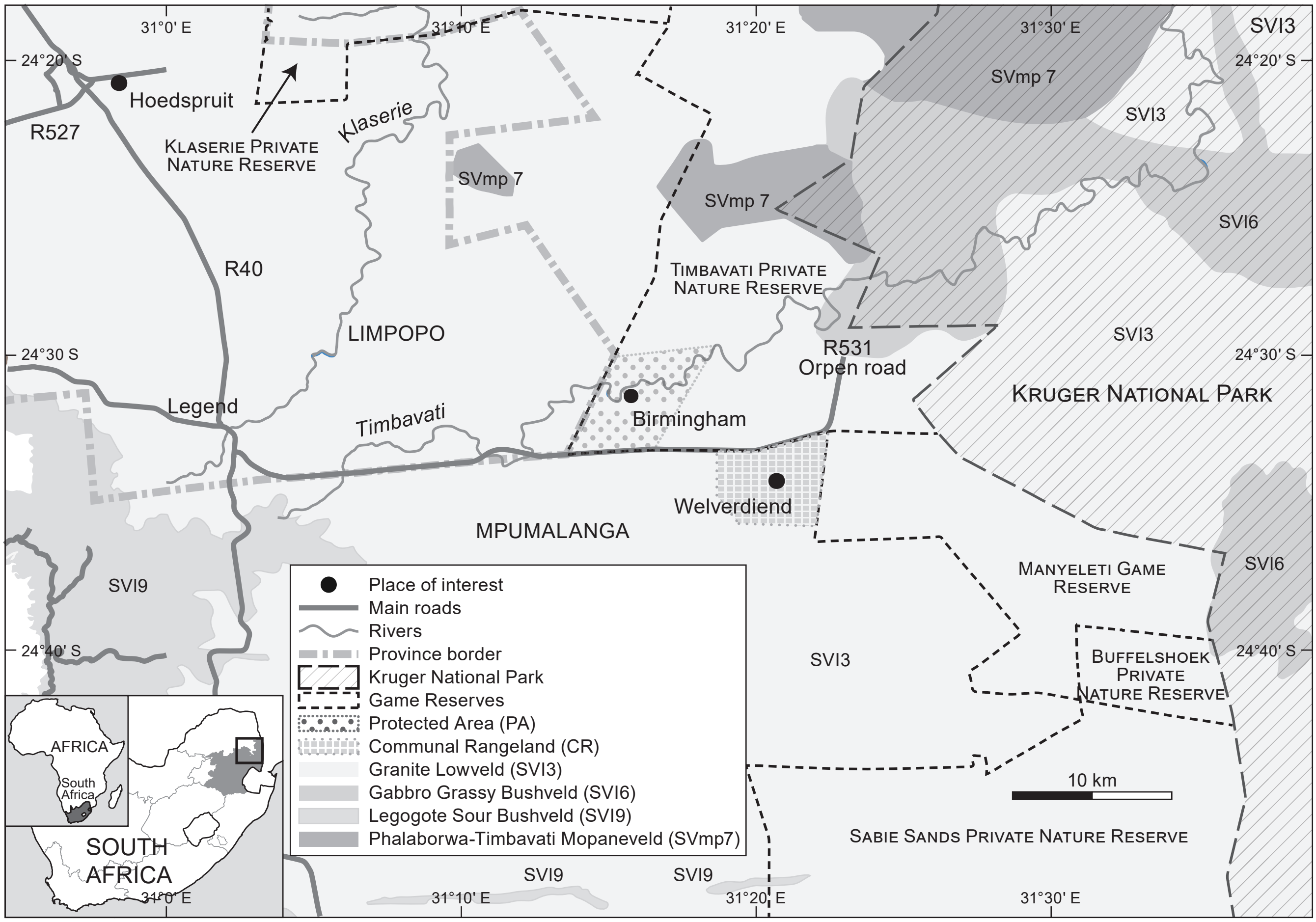

Figure 1: The location of land-use types (Birmingham in the TPNR as the protected area; Welverdiend as the communal rangeland) adjacent to the Kruger National Park in South Africa (courtesy of A Greyling)

study, are characterised by deep sandy soils dominated by broad-leaved woody species, such as *Senegalia nigrescens* (Oliv.) PJH Hurter, *Sclerocarya birrea* subsp. *caffra* (Sond.) Kokwaro, *Albizia harveyi* E Fourn., and several species from the Combretaceae (Mucina and Rutherford 2006). The grass layer is dominated by *Digitaria eriantha* subsp. *eriantha* (Steud.) Maire., *Eragrostis rigidior* Pilg., *Melinis repens* (Willd.) Zizka, *Schmidtia pappophoroides* Steud. ex JA Schmidt*, Urochloa mosambicensis* (Hack.) Dandy and *Aristida congesta* Roem. & Schult., whereas dominant forbs include species from the genera *Commelina*, *Hibiscus, Sida* and several more taxa from the Malvaceae, Fabaceae, Convolvulaceae and Acanthaceae (Mucina and Rutherford 2006).

The climate of the region is semi-arid with a long-term mean annual rainfall of ~630 mm, ranging between 500–700 mm (Kaschula et al. 2005; Matiska et al. 2012). For two consecutive years (2015 and 2016), the entire Central Lowveld (north-eastern Mpumalanga and southern Limpopo) in South Africa experienced below-average annual rainfall (Swemmer et al. 2018). Rainfall for the study sites was ~330 mm below the long-term average for the area in 2015 and in 2016, at the time of floristic sampling. Drought events in the area occur approximately once every 10 years (Matiska et al. 2012), although the drought of 2015 and 2016 was accompanied by extreme temperatures, reaching means of above 30 °C (~8 °C warmer than the mean annual temperature for the area) (Shackleton 1994; Swemmer et al. 2018).

Floristic sampling was conducted towards the end of the drought in October 2016, when rainfall during the preceding months (i.e. total of 22 mm) were less than 50% of the average rainfall received between August and October of 2009 to 2014 (i.e. average total of 49 mm). Sampling was repeated towards the end of January 2017 after more than 150 mm of rain was received in the preceding months, which was close to the average rainfall received for the area between October and January between 2009 and 2017 (i.e. average total of 170 mm). Sampling was conducted within twelve 50 × 20 m fixed plots in each land-use type. The herbaceous layer was sampled in five 1 m^2 subplots positioned along a 50 m centred transect within each of the 1 000 m^2 fixed plots. All forb species rooted within the 1 m^2 subplots (120 in total, 60 in each land-use type) were counted and identified up to species level, conforming to the nomenclature published by Germishuizen and Meyer (2003). Aboveground rooted clonal structures were counted as individuals. Standing herbaceous biomass was clipped and collected at five randomly placed 100 cm^2 plots along the 50 m centred transect line in each 1 000 m^2 plot. Forbs and grasses were separated prior to drying at 30 °C for 24 hours. To quantify the responses of total standing herbaceous biomass (and forb versus grass biomass) to drought release, sampling was done during the drought (October 2016), and repeated after the drought release (January 2017) at each land-use type, respectively.

Data analyses

Non-Metric Multi-Dimensional Scaling (NMDS) analyses were applied to explore forb species assemblages among the two contrasting land-use types, irrespective of rainfall year, to test whether land-use types with contrasting land-use histories host different forb communities. Forb community shifts in response to drought release were furthermore explored for each land-use type, respectively. These analyses were performed in PRIMER 6 (Clarke and Gorley 2006) using Bray–Curtis similarity and fourth-root transformations of species abundances. To corroborate visual representations, Permutational Multivariate Analysis of Variance (PERMANOVA; permutations = 999; type III sums of squares) was applied. PERMANOVA is suitable for abundance data, because response data within complex experimental designs are analysed based on permutations of dissimilarity matrices to make analyses distribution free (Hunter 2017). Permutation analysis of variance does therefore not require specific assumptions for normality (Linstädter et al. 2016). To distinguish between significantly different forb communities across rainfall years, pairwise comparisons of PERMANOVA analyses test, similar to a Tukey test (Scogings et al. 2012), were conducted. To identify the taxa that contributed most to the observed differences in composition, Similarity Percentage Analysis (SIMPER) (Clarke 1993) was applied to the data in Paleontological Statistics software (PAST) (Hammer et al. 2001). Three measures of alpha diversity were selected in this study, which included total species (S), Shannon–Wiener diversity index (H') and Pielou's evenness (J') to account for both richness and evenness as important components of community diversity (Hanke et al. 2014). Diversity values were calculated in PRIMER 6 (Clarke and Gorley 2006). To test for significant responses of forb community diversity, biomass and cover to drought release, parametric paired *t*-tests were performed in SPSS (Version 24) (Hancock and Mueller 2010). Significance levels for analysis were set at the standard significance level of $p < 0.05$.

Results

Forb species composition

The two land-use types hosted significantly different forb communities (Figure 2a; PERMANOVA $F_{(1,117)} = 15.07$, $p = 0.001$), presumably, as a result of the long history of land-use change at the communal rangeland. Significant shifts in forb community composition in response to drought release were revealed for both land-use types (Figures 2b and 2c), although PERMANOVA results revealed stronger community shifts in the protected area ($F_{(1,56)} = 12.616$, $p = 0.001$).

Floristic drivers of forb community shifts were variable across land-use types. Shifts in the protected area were driven mainly by the complete turnover in abundance of both annual and perennial species and not by the dominance of annuals alone (Table 1). At species level, forb abundances in the protected area changed from being absent in the aboveground herbaceous layer during the drought, to post-drought dominance (Table 1). In contrast, species that were responsible for community shifts in the communal rangeland, were more abundant during the drought and included both perennial and annual forbs (Table 1). In contrast to our predictions, only two annuals (*Triumfetta rhomboidea* and *Limeum viscosum*) emerged and co-dominated with two perennials (*Kyllinga alba* and

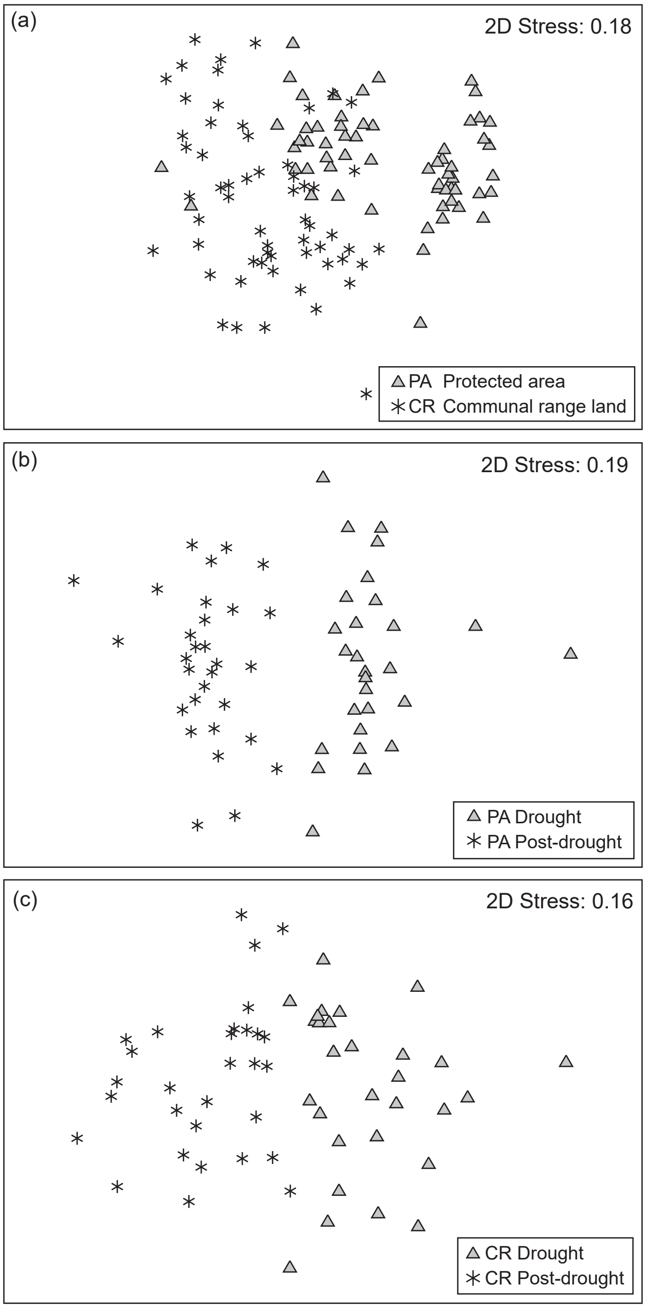

Figure 2: Non-Metric Multidimensional Scaling (NMDS) presentation of forb species composition differences among the contrasting land-use types a), and across rainfall years within the protected area b) and communal rangeland c)

Tephrosia purpurea) in the post-drought forb community of the communal rangeland (Table 1). The cyperoid forb *K. alba* was the only perennial that could maintain its dominance in the communal rangeland. Although not observed during the drought, the perennial legume *T. purpurea* was one of the most abundant species after the drought in both land-use types (Table 1). Four more species that contributed to community shifts were similar across land-use types (i.e. *L. viscosum*, *Chamaecrista absus*, *T. rhomboidea* and *Phyllanthus incurvus*) of which most of these species responded similarly to the drought release. Conversely, the annual legume *C. absus* and the perennial *P. incurvus* were post-drought dominant species in the protected area, but drought dominant species in the communal rangeland (Table 1).

The proportion of perennial forb species increased in 2017 in both land-use types, although the proportion of aliens decreased in both systems in response to the drought release in 2017 (Table 2). Alien forb species accounted for over 16% of the drought-tolerant perennial species in the communal rangeland, which were reduced to 11% in 2017 (Table 2). The proportion of annual forbs decreased in both land-use types. There was an increased contribution of aliens among the annual forb species in the protected area after the drought release, opposed to no annual alien forbs recorded in the communal rangeland after the drought. In the protected area, perennials increased and annual forbs decreased in dominance, although 14% of the most abundant annual species in the protected area were exotic, but non-invasive alien species (Table 2). One third of the drought-dominant forb species in the communal rangeland were perennials, of which 25% were alien species. After the drought release, the proportion of dominant perennial forb species increased, but with a lower abundance of alien perennials (Table 2). Annual forb species, of which 11% were aliens, dominated over perennials in the communal rangeland during the drought, but could not maintain their dominance after the drought release. None of the dominant annual forbs recorded in the communal rangeland in 2017 was an alien species (Table 2).

Biomass and cover

Mean forb biomass was equally low at both rangeland systems during the drought (~29 kg ha^{-1}; Table 3) and increased significantly at both sites after the drought release ($p < 0.05$; Figure 3a), although the increase in the protected area was over three-fold. Grass biomass increased significantly in both land-use types in response to drought release (Figure 3b), although a five-fold increase was reported in the protected area (i.e. from 69 to 325 kg ha^{-1}, Table 3), opposed to a borderline significant increase in grass biomass in the communal area (57 to 96 kg ha^{-1}, Table 3). Forb biomass increases were stronger ($p = 0.005$) than grass biomass increases ($p = 0.021$) in the communal rangeland, but equally strong in the protected area ($p = 0.002$, Table 3). Similarly, forb and grass cover increased significantly in response to the drought release in both land-use types (Figure 3c and d), although in equal magnitudes among the different land-use types (Table 3). Responses to the drought release were much stronger in the grass component, compared with the forb layer productivity (Table 3). Grass-forb biomass ratio in the protected area increased from 69 kg ha^{-1} over 30 kg ha^{-1} during the drought, up to 325 kg ha^{-1} over 94 kg ha^{-1} after the drought release, whereas notably weaker grass biomass dominance was observed in the communal area (i.e. 57 kg ha^{-1} over 29 kg ha^{-1} during the drought, rising up to 96 kg ha^{-1} grass biomass over 64 kg ha^{-1} forb biomass after the drought release) (Table 3).

Table 1: Summary of similarity percentage analyses (SIMPER) results for forb species that contributed to compositional shifts across rainfall years in the protected area and communal rangeland land-use types, respectively

Species	Average dissimilarity	Contributing %	Cumulative %	Mean abundance 2016	Mean abundance 2017	Perennial (P) Annual (A)
Protected area: overall average dissimilarity across rainfall years = 79.6%						
Limeum viscosum	7.9	9.9	24.5	0	104	A
Chamaecrista absus	4.3	5.3	29.8	0	56	A
Bulbostylis hispidula	3.7	4.6	39.1	0	48	A
Triumfetta rhomboidea	3.4	4.3	43.4	0	45	A
**Bidens pilosa*	2.4	2.9	59.6	0	31	A
Hibiscus pusillus	3.7	4.7	34.5	0	49	P
Kohautia virgata	2.8	3.5	46.9	0	37	P
Hermannia boraginiflora	2.6	3.2	53.6	0	34	P
**Richardia brasiliensis*	2.4	3.1	56.6	0	32	P
Phyllanthus incurvus	2.1	2.7	62.3	0	28	P
Tephrosia purpurea	1.6	2.0	66.4	0	21	P
Phyllanthus parvulus	2.7	3.4	50.3	10	46	P
Cyperus rupestris	1.7	2.1	64.4	40	18	P
Gisekia africana	11.6	14.5	14.5	154	2	A
Communal rangeland: overall average dissimilarity across rainfall years = 53.3%						
Tephrosia purpurea	9.9	18.6	18.6	0	146	P
Triumfetta rhomboidea	2.7	5.1	58.0	0	40	A
Limeum viscosum	1.5	2.8	67.7	0	22	A
Phyllanthus maderaspatensis	1.2	2.2	72.4	17	0	P
Schkuhria pinnata	2.0	3.8	61.8	30	0	A
Cleome macrophylla	9.1	17.2	35.8	135	0	A
Monsonia angustifolia	3.2	5.9	52.9	48	1	A
Chamaecrista absus	1.6	3.1	64.9	28	4	A
Phyllanthus incurvus	1.4	2.5	70.2	25	5	P
Kyllinga alba	5.9	11.2	46.9	313	225	P

Table 2: Proportion (%) of total and dominant (i.e. mean abundance value >10) perennial and annual forb species per land-use type during the drought (2016) and after drought-release (2017). Values in brackets represent the proportion (%) of alien species

		Total forb species		Dominant forb species	
		2016	2017	2016	2017
Protected area	Perennials	46 (4)	59 (6)	25 (0)	46 (0)
	Annuals	54 (7)	41 (13)	75 (0)	54 (14)
Communal rangeland	Perennials	49 (16)	54 (11)	31 (25)	54 (17)
	Annuals	51 (5)	46 (0)	69 (11)	46 (0)

Richness, diversity and evenness

Forb richness increased significantly after the drought release in the protected area, but remained comparatively constant in the communal rangeland (Table 3; Figure 4a). Forb species diversity increased significantly in both land-use types, although diversity responses to the drought release were much stronger in the protected area (Table 3; Figure 4b).

Pielou's evenness revealed no significant response to the drought-release for forb communities in either land-use types. (Table 3; Figure 4c).

Discussion

Herbivore assemblages have varying effects on plant communities (Eby et al. 2014; Koerner et al. 2014). Long-term intensive communal grazing in semi-arid ecosystems that have evolved with a diverse suite of grazers and browsers, may function at alternative vegetation states (Parsons et al. 1997; Fynn and O'Connor 2000; Porensky et al. 2013), which explains why forb species assemblages differed among the land-use types, irrespective of the rainfall year. Significant forb community composition shifts after the drought release at both land-use types support previous findings of significant changes in herbaceous communities in response to rainfall variability, irrespective of land-use type (Shackleton 2000; Porensky et al. 2013; Zerbo et al. 2016; Riginos et al. 2018). Semi-arid savanna grazing systems with an annual-dominated herbaceous layer, are known to have a strong post-drought recovery (Ruppert et al. 2015). Forb communities in the protected area displayed a complete turnover in both perennial and annual species abundances in response to the drought release, which was not expected, because it

Table 3: Herbaceous community variables of the two land-use types during the drought (2016) and after the drought release (2017)

Response variable	Land-use type	Mean (±SE) 2016	Mean (±SE) 2017	Paired *t*-test		
				t	DF	*p*
Forb biomass (kg ha^{-1})	Protected area	29.7 (±10.35)	93.8 (±27.04)	−5.98	5	0.002*
	Communal rangeland	28.9 (±11.90)	64.0 (±17.98)	−4.82	5	0.005*
Grass biomass (kg ha^{-1})	Protected area	69.2 (±25.54)	325.3 (±88.58)	−6.28	5	0.002*
	Communal rangeland	56.8 (±4.13)	96.3 (±8.60)	−3.30	5	0.021*
Forb cover (%)	Protected area	2.9 (±1.17)	10.4 (±1.17)	−1.75	29	<0.001*
	Communal rangeland	4.0 (±1.19)	10.2 (±1.19)	−5.22	29	<0.001*
Grass cover (%)	Protected area	3.24 (±0.40)	29.73 (±2.97)	−9.34	29	<0.001*
	Communal rangeland	9.97 (±0.98)	25.87 (±3.44)	−5.14	29	<0.001*
Forb richness (*S*)	Protected area	4.40 (±0.55)	9.50 (±0.55)	−9.36	29	<0.001*
	Communal rangeland	5.17 (±1.77)	5.73 (±1.77)	−1.75	29	0.091
Forb diversity (*H*′)	Protected area	1.21 (±0.10)	1.94 (±0.10)	−7.14	29	<0.001*
	Communal rangeland	1.12 (±0.07)	1.26 (±0.07)	−2.11	29	0.044*
Forb evenness (*J*′)	Protected area	0.87 (±0.03)	0.88 (±0.03)	−0.29	27	0.777
	Communal rangeland	0.73 (±0.03)	0.77 (±0.03)	−1.25	28	0.223

*Significant effects (at $p < 0.05$)

contributed to stronger community shifts, compared with the communal rangeland. These results suggest that, opposed to the communal rangeland where forb community responses to drought release were much weaker, the protected area was able to maintain a viable seed- and bud-bank under disturbance conditions with which the system have evolved (O'Connor and Pickett 1992; Tessema et al. 2012).

In contrast to our predictions, long-term overgrazing combined with drought effects did not deplete forb communities in the communal rangeland, because the species that were responsible for community shifts in response to the drought release were more abundant during the drought year, which included both perennial and annual species. Seeds from annual forb seed banks are known to respond rapidly to sudden moisture increase in the topsoil, albeit local spring rain of less than 5 mm (Ruthven III 2007; Nenzhelele et al. 2018), which was recorded at the communal area a week prior to the 'within-drought' floristic sampling (M Mashele, SAEON, pers. comm. 2016; Kruger National Park Meteorological Records). For this reason, annual forbs, such as *Schkuhria pinnata*, *Cleome macrophylla*, *Monsonia angustifolia*, the legume *C. absus* and the perennial cyperoid *K. alba* were abundant during the drought survey. However, these annual forbs have not been able to withstand two more months of high temperature, drought and browsing by cattle and were therefore unable to flower and set seed for more favourable post-drought conditions to come, which explains the weak responses of annual forbs to the drought release in the communal rangeland. A long history of overgrazing in semi-arid savannas may impose dynamic responses of annual forbs across rainfall years, with a reduction in the emergence of annual forbs after a dry year, as a result of their dependence on spring rain (Nenzhelele et al. 2018) or, as in this case, emergence in response of late spring rain, which caused early dieback, as a result of a lack of follow-up rain. For this reason, our results therefore did not support previous observations of post-drought herbaceous community shifts induced by the emergence

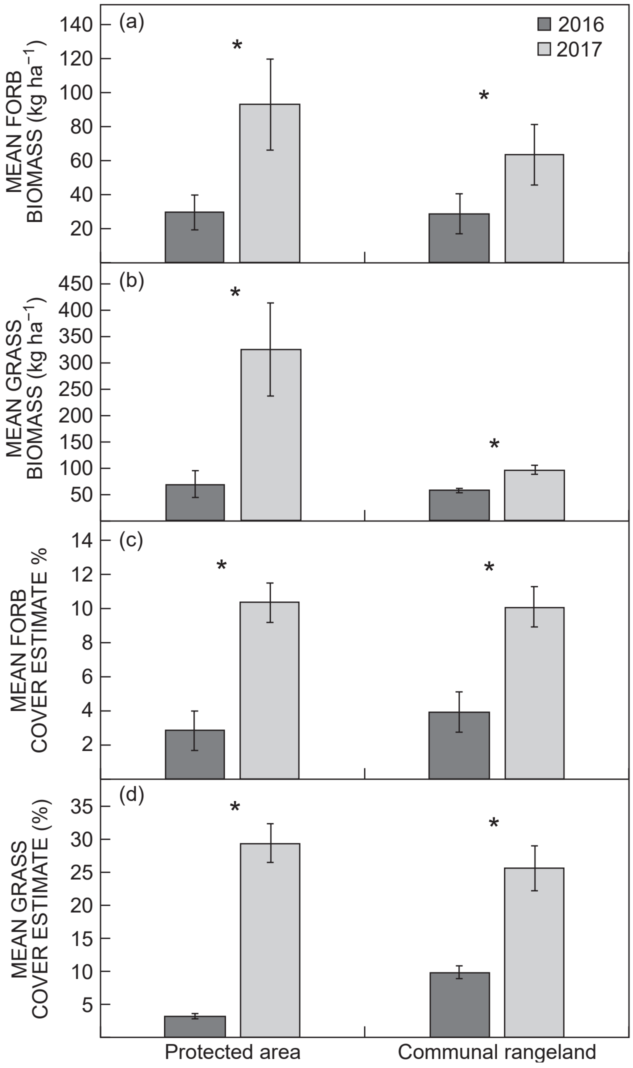

Figure 3: Mean forb and grass biomass a) and b) and cover (c and d) during the drought (2016), and in response to drought release (2017) across two contrasting land-use types. Significant differences ($p < 0.05$) between rainfall years are indicated with an asterisk (*)

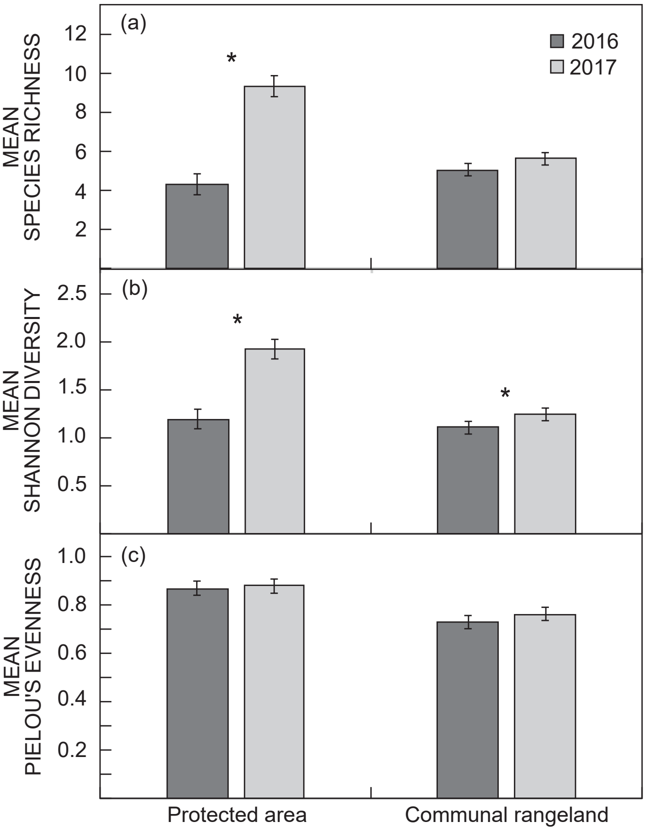

Figure 4: Responses of a) forb richness, b) diversity and c) evenness to the drought release (2017) at the two contrasting land-use types. Significant differences ($p < 0.05$) between rainfall years are indicated with an asterisk (*)

and dominance of annual forbs (Fynn and O'Connor 2000; Morecroft et al. 2004; Vetter 2009; Porensky et al. 2013; O'Connor 2015). However, the long-term, irreversible reduction in herbaceous species seed banks, as a result of sustained heavy grazing (Dreber et al. 2011) may explain the weak increases in forb species richness and diversity after the drought, as well as the much weaker responses of forb biomass opposed to grass biomass.

Forb species that were responsible for community shifts after the drought release represented both perennial and annual life history groups of which the proportion of perennials increased and annuals decreased after the drought in both land-use types. Perennial alien forb species were more dominant during, than after the drought in the communal rangeland. *Alternanthera pungens*, a non-invasive prostrate growing species was among the dominant alien perennials during the drought. This ruderal species is well adapted to tolerate dry and hot conditions through traits, such as small leaves and a prostrate growth form, which is also an adaptation to high grazing pressure (Cornelissen et al. 2003). *Alternanthera pungens* is from the Amaranthaceae, a family known for nutritious resources in Africa (Maundu 1996) and among the several observed severely browsed species during the drought, which explains why it was no longer a dominant species after the drought. Another perennial species that could tolerate intensive dry season browsing in the communal rangeland, *Waltheria indica*, has numerous regenerative buds at a swollen woody stem base (personal observation), which make this species particularly successful during stressed conditions, such as intensive grazing/browsing during a drought (Cornelissen et al. 2003). Forbs in semi-arid savanna ecosystems are expected to be maintained by, not only a viable seedbank, but also a persistent bud-bank, although little is known about belowground functional traits of this dynamic life form (Siebert and Dreber 2019). Traits, such as underground storage organs and a high density of belowground bud-bearing structures are acknowledged to contribute to the understanding of evolutionary pathways and hence, to explain the resilience of forbs to severe periodic disturbances (Pausas et al. 2018), which include drought, fire and herbivore pressure in this particular semi-arid African savanna. There was an overlap in species that were responsible for community shifts after the drought release between the two land-use types. Of these species, the majority responded similarly, although two species, the annual legume *C. absus* and the perennial palatable *P. incurvus* responded inversely at the contrasting land-use types. *Chamaecrista absus* and *P. incurvus* were post-drought dominant species in the protected area (and absent during the drought), but drought-dominant species in the communal rangeland (with very low abundances during the drought-release survey). This may possibly be attributed to the continuous heavy grazing in the communal area, which depleted the seedlings of *C. absus* after emergence during the drought (in response to the local rainfall) and prevented successful regeneration thereafter. Similarly, *P. invurvus*, a perennial forb that makes use of stored resources in its woody rootstock, might not have been able to tolerate the sustained heavy grazing, after which its belowground resources might have become exhausted. *Tephrosia purpurea* responded similarly across the land-use types to the drought release. Its overall contribution to the post-drought forb community in the communal land-use was, however, much stronger than in the protected area, which reflects its high resistance to joint severe disturbances (i.e. livestock grazing pressure and drought). Because nitrogen-fixing herbaceous legumes are becoming more abundant in semi-arid savanna rangelands (Wagner et al. 2016), studies on their belowground regeneration traits are required to improve our understanding of the dynamics and disturbance-tolerance of these important forage species.

The observed low forb biomass and cover during the drought were expected, because such results are common in grazed savanna ecosystems (Porensky et al. 2013; O'Connor 2015). Biomass and cover increases in response to drought-release were, however, lower than predicted, because forbs generally contribute as much as grasses to overall herbaceous cover increases in response to substantial rain following a drought (O'Connor 1991; Porensky et al. 2013; O'Connor 2015). Significant increases in grass biomass and –cover in response to the drought release at both sites are the suggested reasons for weaker increases in forb biomass and cover, as a result of increased competition with emerging forbs. Furthermore, the timing of rainfall in the communal rangeland before the end of the drought, which stimulated forb emergence that could not be maintained through the drought, furthermore explains the unexpected weaker increases in forb cover and biomass opposed to grass biomass and cover increases.

It is well documented that forbs regulate herbaceous species richness and diversity in grassy ecosystems (e.g. Uys 2006; Bond and Parr 2010; Koerner et al. 2014; Scott-Shaw and Morris 2015; Siebert and Scogings 2015), as a result of a diverse pool of traits that allows for a variety of adaptive strategies (Uys 2006; Hanke et al. 2014). Despite this, forb species richness and diversity were equally low at the two land-use types during the drought, although post-drought conditions enhanced the richness and diversity of forbs, despite higher grass biomass and -cover. These results are in accordance with similar studies that reported increases in herbaceous species richness and diversity with increased precipitation (Cleland et al. 2013; Porensky et al. 2013; Koerner and Collins 2014; Zerbo et al. 2016). Although communal lands have been reported to host higher species richness than adjacent conservation areas in a similar semi-arid savanna ecosystem (Shackleton 2000), post-drought conditions in the communal rangeland had a weak effect on species richness, compared with the protected area. The diversity of herbivores in the protected area promotes diverse foraging patterns, (Du Toit 2003; Codron et al. 2007), which allow for dispersed herbivore effects and hence, more species to coexist (Van Coller et al. 2018). Furthermore, the high functional trait diversity of forbs in systems that evolved with natural disturbances, such as herbivory and drought, (Hanke et al. 2014; Van Coller and Siebert 2019) may explain the increases in forb species richness and diversity in the protected area in response to the drought release. The strong forb community responses in the protected area suggests that the species that emerged after the drought-release may be less drought tolerant (i.e. they were absent during the drought survey), but rather drought avoidant through escaping the effects of the drought through a persistent seed-, or bud-bank. Because emergence patterns of forbs in response to disturbances are species- and functional trait-specific (Siebert and Dreber 2019), long-term intensive grazing may have filtered out the majority of drought avoidant species and –traits and benefit forb species and -traits that are drought-tolerant under sustained grazing pressure (Dreber et al. 2011).

As components of community diversity measures, evenness and dominance are important measures to understand ecosystem processes and hence, to explain particular community responses to disturbances (Hillebrand et al. 2008; Koerner et al. 2018). Forb species evenness was expected to decrease after the drought at both land-use types, because herbaceous community shifts following a disturbance event are mostly driven by dominance of opportunistic species (O'Connor 2015). Furthermore, drought-induced grass tuft mortality in a heavily grazed system allows annual forbs to colonise the area (O'Connor 1995; Fynn and O'Connor 2000; Porensky et al. 2013), which may cause a shift in dominance during post-drought conditions. Our results, however, revealed weak rainfall effects on forb evenness at both land-use types, which suggest weak dominance of by a limited number of species during and after the drought.

Conclusions

The observed forb community dynamics during, and directly after an extreme drought event emphasised that contrasting land-use types with divergent herbivore assemblages, herbivory pressure and duration of disturbance impacts may reveal both similar and conflicting results. Such results are, however, expected when a species- and functionally diverse, and ecologically dynamic life form is being investigated. To illustrate this, neither land-use types displayed a remarkable emergence of annual forbs in response to the drought release, despite multiple studies on post-drought dominance of annual forbs. This highlights the importance of considering species-specific adaptive traits, rather than life history only when investigating forb community responses to environmental perturbations. Despite several unexpected response patterns, our results added to our understanding of the combined effects of drought and herbivory on forb communities at two opposite end of land-use type disturbances. Because frequencies of drought events in African savannas are expected to increase while diverse herbivore communities are under increasing pressure, attempts to manage savanna rangelands for long-term ecosystem resilience are becoming more important. Forb communities in the communal rangeland land-use type were relatively stable, although our results revealed that a moderate level of mixed herbivore community grazing and browsing may promote a more balanced suite of species with both disturbance-tolerant and –avoidance traits through healthy seed- and bud banks. Additional research is, however, required to better understand trait-specific filtering of forb species among contrasting land-use types. Finally, this study emphasises that past effects, albeit a short-term, localised natural stress release, or long-term high grazing pressure, regulate observed patterns in forb community dynamics and have to be considered to fully understand forb community responses to disturbances.

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