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Climate variability in the Woodbush Granite Grasslands of South Africa: Effects on grassland diversity

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Key words: Grassland diversity; drought; fragmented pristine grassland; gains; losses; abundance; occurrence

Abstract

South African old-growth grasslands are hyper-diverse ecosystems which evolved under naturally occurring rainfall variability. It is predicted that future precipitation patterns will become more variable, which could lead to increased frequencies of extreme and prolonged drought events. This study aimed to investigate the effects of climate variability on plant diversity of the fragmented pristine, mistbelt grasslands of the Woodbush Granite Grasslands (WGG) at Haenertsburg, South Africa. It has been reported that species composition has changed substantially in this area, as disturbance-tolerant species enter these systems or existing competitor species become more dominant. A Temporal Beta-diversity Index (TBI) was used to determine the gains and losses in taxonomic and functional diversity, and of endemic and threatened species since 2009. Results show that there was a gain in species from before (2009) to onset of drought (2015) and a loss in species from the onset of the drought (2015) to after the drought (2019), while the overall effect of the drought on species occurrence from 2009 to 2019 was non-significant suggesting ecosystem resilience to drought.

Introduction

The old-growth grasslands of South Africa evolved in the presence of the endogenous disturbances, such as lightning-ignited fires, rainfall variability and large mammalian herbivory (Buisson et al, 2019; Koerner and Collins 2014). For this reason, grassland ecosystems are tolerant and to some extent dependent upon these natural disturbances (Buisson et al. 2019).

Drought is a natural occurring phenomenon characterized by changes in precipitation, soil moisture, groundwater and streamflow (Botai et al. 2019). During November of 2015 to April of 2016, most parts of South Africa experienced a severe drought during the rainy season (Yuan et al. 2018). This seasonal drought was intensified by heat waves and a soil moisture deficit (Yuan et al. 2018).

It is expected that drought events may become more frequent in years to come (IPCC 2012, Hoffman et al. 2019) with associated warmer temperatures and declines in annual rainfall (Bodner and Robles 2017). Studying the impact of drought on grasslands has gained urgency as there is a need to understand how droughts will impact the sustainable management of grasslands now and in the future (Bodner and Robles 2017). Therefore, an improved understanding of the floristic and functional diversity is necessary to understand the community and functional shifts related to climate change.

The objectives of this study were to assess floristic changes related to rainfall variability in Woodbush Granite Grassland (WGG) through the application of the Temporal Beta-diversity Index (TBI) with a particular focus on taxonomic diversity, and endemic and threatened species.

Methods and Study Site

A diverse, but threatened grassland type in South Africa, the WGG, was selected to test the effects of rainfall variability on grassland diversity and function. The WGG occurs around Haenertsburg within the Mesic Highveld Grassland Bioregion of the Grassland Biome and forms part of the Wolkberg Centre of Endemism (Van Wyk and Smith 2001). This grassland type is listed as a Critically Endangered ecosystem since only about ~6% is still in a natural state (Mucina and Rutherford 2006). The largest remaining fragment of WGG is only 192 ha (Dzerefos et al. 2017), which is surrounded by multiple land-use types. The WGG borders the Sour Bushveld vegetation of the Savanna Biome to the east (Mucina and Rutherford 2006), which is anticipated to expand and encroach into WGG as a result of climate change (i.e. drier, warmer climate and increased atmospheric CO_2) (Bond and Midgley 2000; Bond and Midgley 2001; Clarke et al. 2013). Embedded

in the grassland are patches of Northern Mistbelt Forest. Since the WGG is critically threatened and the remaining fragments very small, the conservation value of the area is high.

The South African Environmental Observation Network (SAEON) has erected 40 permanent annual burn vegetation monitoring plots in the WGG. These plots have been monitored since 2009, and baseline vegetation data have been collected to compile a floristic dataset. The sampling and data collection conforms to the SAEON sampling protocol for long-term grassland monitoring, i.e., permanent plots have a size of 4 x 4 m, and are divided into 16 smaller subplots of 1 m² each. In the four corner subplots of the 16 m² plot, the percentage aerial cover of grass, forb and woody species was recorded. Thus, a total of 160 subplots was sampled during each sampling event. Sampling was done in February, i.e., at the time of peak standing crop. Sampling was done in the years 2009, 2015 and 2019. During this observation period, a severe drought occurred in 2015. The tree sampling events thus represent pre-drought (2009), drought (2015) and post-drought conditions (2019).

Non-Metric Multi-Dimensional Scaling (NMDS) analysis in Primer (2007) explored changes in species composition between sampling events 2009, 2015 and 2019. To determine whether significant differences in plant assemblages exist over time, Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using species abundance data. Analyses were conducted with 999 permutations using Bray–Curtis similarity and type III sums of squares after a square-root transformation of species data to reduce the influence of common species. Single factor ANOVA tests were applied to test for significant differences between 2009, 2015 and 2019 for selected diversity measures.

According to Legendre (2019), aerial cover data can be treated as species abundances in the Temporal Betadiversity Index (TBI) test. The TBI calculations were implemented in the *TBI.R* function available in the package *adespatial* of the R software (version 4.0.2). The percentage difference (%diff), also known as the Bray-Curtis dissimilarity index, was used as it contains the proxies *B* and *C*, which represent the species loss and gain components of dissimilarities (Legendre 2019). B-C plots (Fig. 1) were created with the *B*/den and *C*/den statistics as coordinates of points, representing sites. These graphs visually display the relative importance of the loss and gain processes across time. The function *tpaired.krandtest.R* was used to identify the species abundances that have changed significantly between T1 and T2 (Legendre 2019).

Results

The aerial cover of 261 species was determined across 160 subplots, which included 45 grass species, 173 forb species and 43 long-lived forb and woody/shrub species. Of these species, 14 were South African endemics (5%), three endangered (1%) and one near threatened. The most prominent families were the Asteraceae (19%), Poaceae (15%) and Fabaceae (13%).

The results from the NMDS revealed separate clusters for the three years, 2009, 2015 and 2019 (Fig. 1). These annual clusters were verified by PERMANOVA (df = 2, pseudo-F = 16,017, p = 0,001), which indicated a significant difference in floristic composition between years. The species that contributed most to these changes from 2009 to 2019 are the grasses *Cymbopogon nardus* (L.) Rendle, *Loudetia simplex* (Nees) C.E.Hubb., *Setaria sphacelata* (Schumach.) Moss and *Themeda triandra* Forssk., and the forbs *Acalypha peduncularis* E.Mey. ex Meisn., *Berkheya setifera* DC. and *Helichrysum nudifolium* (L.) Less.



Transform: Fourth root					
Resemblance: S17 Bray Curtis similarity					
3D Stress: 0,21					
WGG 2009-2019					
A 2009					
v 2015					
2019					

Figure 1: Non-Metric Multidimensional Scaling (NMDS) ordination for 2009 (pre-drought), 2015 (onset of drought) and 2019 (post-drought) plots with species abundance data.

Species richness and diversity was expected to be affected by the drought conditions of 2015. Single factor ANOVA tests revealed significant changes for all diversity measures (i.e., J', H' and S) for the three years (p<0.001, Table 1).

Measure	2009	2015	2019	df	F	р
Pielou's evenness (J')	$0,77\pm0,007$	$0,797 \pm 0,003$	$0,77\pm0,005$	2	7,42	< 0.001
Shannon Diversity Index (H')	$2,182 \pm 0,144$	$2,404 \pm 0,085$	$2,191 \pm 0,097$	2	23,15	< 0.001
Total species (S)	$17,3 \pm 17,2$	$21,0 \pm 23,8$	$17,5 \pm 12,8$	2	39,09	< 0.001

Table 1: Mean values (±SD) of selected diversity measures for pre-drought (2009), at the onset of drought (2015) and post-drought (2019) conditions. Significance was set at p < 0.05.

In the B-C plots (Figure 2), the diagonal green line (slope = 1) goes through the origin, and represents the theoretical positions of sites where the gain would be equal to the loss (Legendre 2019). The red line, parallel to the green line, passes through the centroid of all points (Legendre 2019). When the red line is below the green line, it indicates that species loss dominated across the sites, with the opposite being true if the red line is above (Legendre 2019). Furthermore, points found toward the upper-right corner represent higher temporal beta diversity than points found toward the lower-left corner (Legendre 2019).

The function *tpaired.krandtest*. R revealed the following: Threatened and endemic species that significantly contributed to the changes observed in Figure 1 include the near threatened species Merwilla plumbea (Lindl.) Speta which significantly increased in occurrence from 2009 to 2015 and significantly decreased in occurrence from 2015 to 2019; the endemic species Alepidea peduncularis A.Rich. which significantly decreased in occurrence from 2009 to 2019; Pygmaeothamnus chamaedendrum (Kuntze) Robyns var. chamaedendrum which significantly increased in occurrence from 2009 to 2015; Senecio pentactinus Klatt which significantly decreased in occurrence from 2015 to 2019 and Argyrolobium transvaalense Schinz which significantly decreased in occurrence from 2009 to 2015.



- Significant woody species = 7
- Significant woody species = 5

- Significant woody species = 7



Figure 2: B-C plots of all species occurrences (presence-absence) (top) and all species abundances (bottom) of the 40 annually burnt plots, before (2009), and at the onset (2015) and after (2019) the drought. Squares represent plots where gains dominate and circles represent plots where losses dominate.

Discussion

We assumed that a severe drought would trigger a substantial loss of plant diversity. However, our results do not support this assumption. There were significant differences (p<0.001) between years for all diversity measures (J', H' and S; Table 1) when 2009 was compared to 2015, and 2015 to 2019. However, no significant differences were observed when the years 2009 (pre-drought) and 2019 (post-drought) were compared (p>0.001). This indicates that the WGG system is quite resilient, and in accordance with a growing body of work that supports the idea that biodiversity promotes ecosystem functioning and stability (Mori et al. 2013).

The TBI analysis for species occurrences supports the idea that the WGG system is resilient to drought, as there was an overall gain in species from 2009 to 2019, even though it was not significant. This means the gains and losses of species seem to compensate each other, as the mean number of species (Table 1) was similar pre- and post-drought. It has been observed that the effect of drought alone on grasslands had a minimal impact on plant community structure and composition (Koerner and Collins 2014). The combination of drought with other disturbances, such as fire and grazing, could have a more significant effect on grassland communities as observed for savanna (Siebert et al. 2020).

It was expected that the drought would result in loss of species, but it appears that the drought rather impacted the abundances of species more severely. Even though there was a significant loss in abundance of species from 2009 to 2019, it has been observed that vegetation in southern Africa has either remained stable or has increased in cover and biomass over the course of the 20th century (Hoffman et al. 2019). It is therefore expected that the abundance of species will recover over time to be similar to that experienced before the drought event.

It would appear that the species in the WGG are to some extent drought tolerant, which would be a benefit to the system as grasslands without drought-tolerant species would likely experience major declines in ecosystem functioning during times of drought (Craine et al. 2013). This knowledge could aid our understanding of the distribution of drought tolerant plants in order to better predict future responses and resilience to climate change (Craine et al. 2013).

This study set out to assess the impact of a severe, multiple-year drought event on the floristic diversity of a biodiverse South African grassland. Unexpectedly, the drought event did not have a strong effect on species occurrence from 2009 to 2019. However, there was a decrease in species cover and slight changes in species composition. Further studies are needed to determine the effect of severe drought events on grasses, forbs and

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