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South African mesic grasslands are resistant to drought but not warming

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Abstract

Current climate change models predict increases in temperature, reduced frost and more variable rainfall with increased frequency of extreme weather events such as flooding and drought. Southern Africa is expected to experience more frequent drought, and the grassland biome expected to be significantly affected by this. A possible reduction in area of between 30 and 50% is predicted. Given the importance of the grassland biome from both an intrinsic and economic perspective this reduction could have serious economic and food security consequences. For these reasons, it is critical to increase our understanding of ecosystem processes under drought-stress and warming. In winter 2019 a rainfall exclusion and warming trial was established in a good condition mesic grassland in KwaZulu-Natal, South Africa. Rainout shelters reduced the incoming precipitation by 53% and open-topped chambers increased daytime air temperature by 2°C. Species abundance data was collected annually. Rainfall manipulation had a marginal effect on species composition, however warming resulted in reduced abundance of several common forbs and the loss of numerous forb and grass species, also reducing species richness. Simpson's diversity was unaffected. These reductions in species richness reduce the ability of the grassland to recover from climatic perturbations and thus rainfall reduction coupled with warming presents a significant threat to grassland ecosystem services.

Introduction

In South Africa, the grassland biome is the second most diverse, after the fynbos biome, and contains many rare and threatened species (Rutherford & Westfall 1994). However, almost 60% of the grassland biome has been modified through development and crop production (Low and Rebelo 1998) and less than 3% is conserved (SANBI 2013). The remainder is used for livestock production, predominantly cattle and sheep (SANBI 2013). After modification and degradation, the second major threat to grasslands is climate change (SANBI 2013). Current climate change models predict increases in temperature, reduced frost and more variable rainfall with increased frequency of extreme weather events such as flooding and drought (IPCC, 2022). Data gathered since 1950 has shown increased CO_2, temperatures, and frequency of extreme climatic events (IPCC 2012). Southern Africa is one of the regions expected to experience more frequent, long-lasting drought and heat waves (Trisos et al. 2022 in IPCC, 2022). This will significantly affect the grassland biome, possibly reducing the area by between 30 and 50% (Mucina and Rutherford 2006). Given the importance of the grassland biome from both an ecological and economic perspective this reduction could have serious economic and food security consequences (Kapuka & Hlásny 2021, Miranda et al. 2009). For these reasons, it is critical to increase our understanding of ecosystem processes under warming and drought-stress.

Methods

The trial was established using the Drought-Net Research Coordination Network standard protocols (Smith et al. 2024), where clear plastic roof sheeting was used to impose a statistically extreme, 1-in-100 year drought. Nine plots (5 x 3.5 m, with six 1 m^2 subplots) were arranged in a split-plot, randomised block design in a section of good-condition natural veld at the Ukulinga Research Farm, University of KwaZulu-Natal (30°24′ S, 29°24′ E). The farm has summer rainfall with a mean annual precipitation of 838 mm and a mean annual temperature of 18 °C (Ward et al. 2020). The plots were established in 2019, with the 2019/2020 growing season being the first treatment year. Rainfall manipulation took place at the whole plot level and warming at the subplot level. The rainfall manipulation treatments were drought (53% reduction), ambient and run-on (diversion of intercepted rainfall from drought). Warming was applied on a single subplot using hexagonal open-topped warming chambers made from 2 mm thick clear polycarbonate sheeting (Mu et al. 2017), resulting in an average daytime temperature increase of ~2 °C. Species composition was surveyed at the beginning of the growing season (early December) and at the peak of the growing season (late March). Maximum abundance per species was used for data analysis. In dedicated destructive sampling subplots (for rainfall manipulation only), biomass was harvested after the last rains (late April/early May) and separated into functional groups. Data analysis was conducted in R statistical software (version 4.2.0) and R studio (version 2024.9.1.394) using packages *vegan* (Oksanen et al. 2024) and *dplyr* (Wickham et al. 2023) and plots created using *ggplot* (Wickham et al. 2016) and *ggrepel* (Slowikowski 2024.). Changes in species composition between the first (2020) and the fifth (2024) treatment years were assessed using PERMANOVA and visualised using a partial canonical correspondence analysis. Data were log transformed to reduce the influence of rare species. When PERMANOVA revealed significant effects, a SIMPER analysis was conducted to identify the species contributing to the differences. Differences in species richness and Simpson's diversity were assessed using repeated measures ANOVA.

Results

After five years of treatment application PERMANOVA revealed significant effects of year and warming on species composition (Figure 1 a&b). There was a marginal effect of moisture level ($p = 0.051$) but no significant treatment interactions. SIMPER analyses ($p > 0.05$) indicated that the differences between 2020 and 2024 were driven by decreases in the abundance of two grass species (one palatable and one acceptable), which were replaced by increases in two palatable grass species. Warming resulted in two to three-fold reductions in abundance of three common forb species and an eight-fold reduction in abundance of one acceptable grass species. In addition, five grass and fifteen forb species occurring in low abundance were lost due to warming.

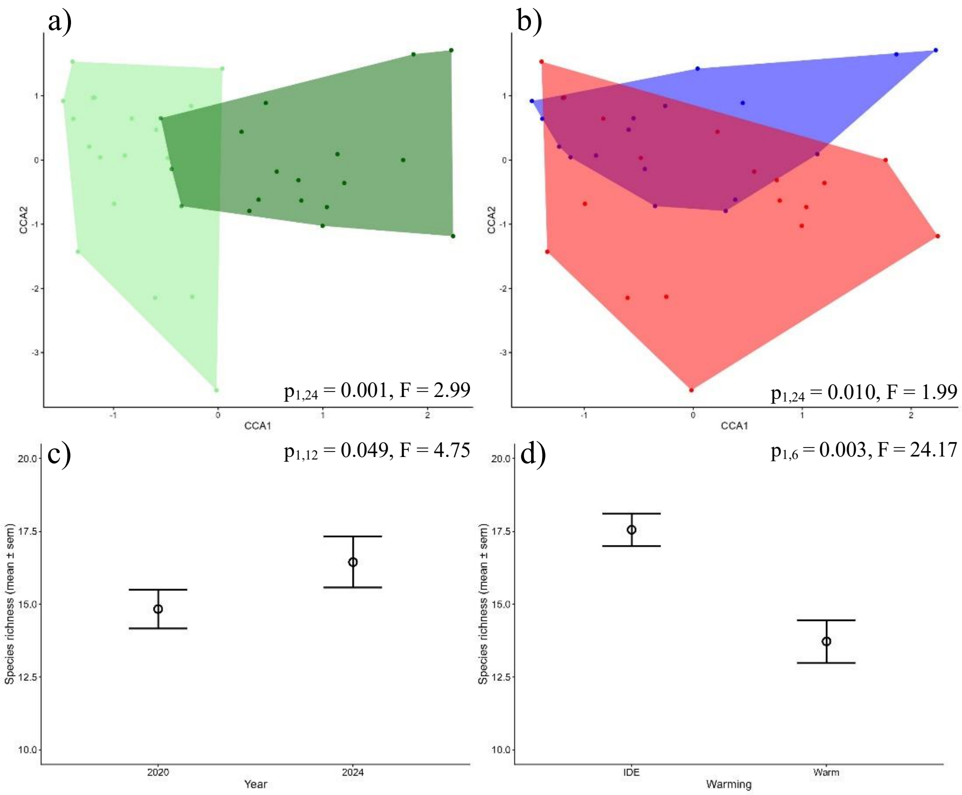

Figure 1: Partial Canonical Correspondence Analysis (pCCA) biplots showing the relationship between species composition (a) Year (2020 in light green and 2024 in dark green), (b) Warming (IDE/unwarmed in blue and warmed in red) after accounting for spatial effects using blocking. Eigenvalues of the axes (CCA1 and CCA2) are 0.218 and 0.171, explaining 18.48% and 14.51% of the constrained variation, respectively. The analysis was conducted after a significant PERMANOVA. The effect of (c) Year and (d) Warming on mean (± SE) species richness after a repeated measures ANOVA revealed significant effects.

Simpson's diversity showed no significant effects. Species richness was also significantly affected by year and warming. Overall species richness increased from 2020 to 2024, while warming reduced species richness compared to ambient conditions (Figure 1 c&d).

Discussion

The distribution of the grassland biome is strongly driven by climate, occurring across a rainfall range of 400 – 2000 mm (Department of Environmental Affairs 2015, Mucina and Rutherford 2006). Mesic grasslands are currently predicted to become 10 – 15% drier (Department of Environmental Affairs 2015). This level of rainfall reduction has been found to significantly reduce grassland productivity and diversity (Miranda et al. 2009), however, the duration of drought has a greater impact on the ecosystem than the intensity (Sala et al. 2015). Single-year drought studies tend to produce more variable responses than multi-year studies (Griffin-Nolan et al. 2018, Petrie et al. 2018) but in general, drought reduces productivity (Balachowski and Volaire 2018) through altered species composition and tuft morphology, and reduction in basal cover. Over the last 14 years, annual rainfall in the study site was observed to fluctuate by over 250 mm above and below the long-term annual mean of 838 mm (unpublished data). The lack of response observed over five years of rainfall reduction is likely due to the adaption of these mesic grasslands to regular rainfall fluctuations, however, with extended exposure to drought the vegetation is expected to lose this resilience (Midgely et al 2011).

The reduction in species richness observed after five years of warming to 2° C above ambient supports the predictions made by SAEON (2015). Since species richness is expected to influence the capacity of the vegetation to withstand and recover from perturbations like droughts (Van Ruijven & Berendse 2010) the combination of warming and long-term exposure to drought puts these grasslands at risk of degradation and woody invasion through reduced fire frequency and intensity. By contrast, diversity was unaffected, likely because the dominant species were unresponsive to the treatments.

Although South African mesic grasslands have been resilient to five years of extreme drought, they have suffered significant degradation through species loss because of warming. Extended exposure to drought, particularly given the marginal significance observed after five years of rainfall reduction, coupled with warming is expected to cause future vegetation degradation. This will result in the loss of numerous ecosystem services which are likely to have economic and food security consequences. This response observed in mesic grasslands, near the centre of the biome's rainfall range, is concerning and highlights the need for research closer to the limits of the rainfall range as these areas are likely to exhibit more rapid and extreme responses.

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