Rapid recovery of ecosystem function following extreme drought in a South African savanna

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Abstract:

Climatic extremes, such as severe drought, are expected to increase in frequency and magnitude with climate change. Thus, identifying mechanisms of resilience is critical to predicting the vulnerability of ecosystems. An exceptional drought (<first percentile) impacted much of southern Africa during the 2015 and 2016 growing seasons, including the site of a long-term fire experiment in Kruger National Park, South Africa. Prior to the drought, experimental fire frequencies (annual, triennial, and unburned) created savanna grassland plant communities that differed in composition and function, providing a unique opportunity to assess ecosystem resilience mechanisms under different fire regimes. Surprisingly, aboveground net primary productivity (ANPP) recovered fully in all fire frequencies the year after this exceptional drought. In burned sites, resilience was due mostly to annual forb ANPP compensating for reduced grass ANPP. In unburned sites, resilience of total and grass ANPP was due to subdominant annual and perennial grass species facilitating recovery in ANPP after mortality of other common grasses. This was possible because of high evenness among grass species in unburned sites predrought. These findings highlight the importance of both functional diversity and within-functional group evenness as mechanisms of ecosystem resilience to extreme drought.

Keywords: ANPP | climate extreme | evenness | fire | functional diversity | precipitation | resilience

Article:

Introduction

Empirical data and model projections suggest that regional-scale droughts are increasing in frequency, duration, and magnitude across the globe (Dai 2012, Trenberth 2012, Cook et al. 2015). These more severe and prolonged droughts have the potential for large and long-lasting effects on ecosystem structure and function (Du et al. 2018, Sankaran and Staver 2019). To maintain function in response to extreme drought, ecosystems must exhibit either high resistance during drought (e.g., limited loss of function) or high resilience following drought (e.g., rapid recovery). Most ecosystems have low resistance to drought (Stuart-Haëntjens et al. 2018), and the high likelihood that future droughts will fall outside historical norms (Cook et al. 2015) makes it improbable that ecosystem function will be maintained through resistance alone. As such, resilience to extreme events is likely to be critical for maintaining long-term ecosystem functioning. To promote and maintain resilience of ecosystem function after extreme events, we require better understanding of the mechanisms promoting it.

Ecosystem resilience to drought may occur through two fundamentally different mechanisms: (1) through compensatory dynamics such that drought-tolerant plants increase in abundance and functionally compensate for declines in drought-intolerant species (Elmqvist et al. 2003, Gonzalez and Loreau 2009, Lloret and Escudero 2012, Hoover et al. 2014, Gherardi and Sala 2015), or (2) through physiological compensation whereby all individuals within the community recover fully after drought (Connell and Ghedini 2015). Physiological compensation will likely be important during short-term, moderate drought, but compensatory dynamics driven by reordering of species abundances are more likely to occur under extreme, prolonged drought (Smith 2011).

Grasslands, which cover ~40% of the terrestrial land surface and provide critical ecosystem functions and services (Lemaire et al., 2011), are expected to be particularly vulnerable to intensified droughts, given the high sensitivity of ecosystem productivity to water availability (Huxman et al. 2004). A recent meta-analysis suggested that rapid resilience, rather than resistance, maintained ecosystem productivity in grasslands following extreme drought (Stuart-Haëntjens et al. 2018). Yet the determinants of grassland resilience to extreme drought remain poorly resolved. Grasslands are generally composed of two dominant herbaceous functional groups—grasses and forbs—which differ widely in their vulnerability to extreme drought (e.g., Taylor et al. 2011). In many grasslands, grasses are better able to tolerate drought because of their C_4 photosynthetic machinery (Ward et al. 1999), whereas forbs may avoid drought conditions via deeper rooting profiles (Nippert and Knapp 2007). Within both of these categories, however, responses during and after drought may be different between annual and perennial species (Volaire 2003, Vetter 2009). Thus, postdrought resilience in grasslands may depend on functional diversity in predrought communities.

Fire is an important global attribute of grasslands that can alter the relative abundance of grasses and forbs, with frequent fire promoting dominance by C_4 perennial grasses (Collins et al. 1998, Bond et al. 2003, Smith et al. 2016). Thus, fire frequency is likely to be an important mediator of ecosystem resilience to extreme drought by affecting the relative contribution of grasses and forbs to compensatory dynamics. Little is known about this potential interaction between fire and drought. In a frequently burned mesic C_4-dominated grassland (tallgrass prairie in Kansas, USA),

experimentally imposed extreme drought resulted in a loss of forbs with rapid recovery of aboveground net primary productivity (ANPP) postdrought because of increased abundance of grasses (Hoover et al. 2014). However, in the same C_4-dominated grassland, wildfire during a naturally occurring extreme drought increased forb abundance postdrought (Ratajczak et al. 2019). Furthermore, Koerner and Collins (2014) showed that shifts in grass and forb relative cover were minimal in both mesic grasslands in North America and South Africa under short-term experimental drought across different fire regimes. Together, these results suggest that the grass and forb components in C_4-dominated grasslands may play different roles in resilience to drought depending on the interactive effects of fire and drought severity, and these interactions may differ across ecosystems.

During the 2015/2016 growing seasons, South Africa experienced one of the worst droughts on record, with large socioeconomic impacts occurring in much of Southern Africa (Baudoin et al. 2017). In the central region of Kruger National Park (KNP), where drought severity was greatest, we had the unique opportunity to examine how fire frequency interacted with extreme drought in this ecosystem, and how grass and forb functional groups affected postdrought resilience. In the C_4-dominated herbaceous component of this savanna grassland, we measured aboveground productivity and species abundance within permanent plots located in annually, triennially, and unburned sites for 9 yr (2006–2014) prior to the drought and again the year after the extreme drought ended (2017). Using these data along with remote-sensing data before, during, and after the drought, we asked two questions: (1) Is ecosystem productivity resilient to extreme drought and does resilience vary with fire frequency? (2) What role do grass and forb functional groups play in postdrought resilience and does this role vary with fire frequency?

Methods

Site description

KNP is a 2-million-ha protected area located in northeastern South Africa. The Experimental Burn Plots were initiated in KNP in 1954 to examine the effects of fire frequency on vegetation; here we focus on unburned, 3- (triennial), and 1- (annual) year fire return intervals (Biggs et al 2003). Fire treatments within Experimental Burn Plots are each ca. 7 ha in size and triennial and annual treatments are burned in August during scheduled years, coinciding with the end of the dry season. Our research occurs in central KNP on two Experimental Burn Plots (Satara and N'wanetsi), which we treated and refer to hereafter as separate blocks. Here, mean annual precipitation for the period 1937–2017 was 547 mm hydrological per year (1 July–30 June) and the mean monthly maximum air temperature was 29°C in January (early growing season, Venter et al. 2003). Soils are fine-textured, clayey, and largely uniform throughout the area (Venter et al. 2003). The vegetation is characterized as Knobthorn–Marula savanna, which has a dense layer of perennial C_4 grasses, dominated by *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, *Panicum maximum*, and *Themeda triandra*, along with the presence of numerous annual and perennial forbs. We established exclosures to exclude herbivores >0.5 kg (38.5 m^2 each, Appendix S1: Fig. S1) in both blocks prior to the 2006 growing season (Koerner et al. 2014). Each of the three burn frequencies contained $n = 7$ exclosures at each of the two blocks ($n = 2$; 538.5 m^2 excluded from herbivory per burn per block; Appendix S1: Fig. S2).

Precipitation and enhanced vegetation index (EVI)

Daily precipitation data since 1937 were collected from the Satara weather station (24°23′49.33″ S, 31°46′39.04″ E). Monthly precipitation totals were calculated for each hydrological year (1 July–30 June) and used to calculate long-term mean annual precipitation. Hereafter, reference to precipitation in a particular hydrological year indicates precipitation falling between 1 July of the previous year and 30 June of the indicated year. Precipitation data were also used to calculate the Standardized Precipitation Index (SPI) on 12-month timescales. Briefly, total precipitation for every 12-month window from 1937 to 2017 was calculated to create a normally distributed probability density with a mean of zero and standard deviation of unity. SPI values <-2 represent 12-month time windows considered to be "extreme," occurring ca. 2.3% within the precipitation record used. See McKee et al. (1993) for additional details on SPI. To examine trends in drought severity, we focused on "extremely dry" events (SPI <-2, $n = 10$), where an event was defined as a period of time where SPI was continually <-2. Drought severity of an event was calculated as the sum of SPI over that interval (McKee et al. 1993).

EVI trends were assessed in addition to ANPP measurements because field measurements of ANPP were not collected in 2015 or 2016. We used EVI from 2000 to 2017 as a proxy for live vegetation biomass throughout the years before, during, and after the 2015/2016 drought. We used MODIS products from the Terra and Aqua MODIS satellites (Didan 2015) to obtain EVI estimates every ca. 8 d throughout the year from nine 250 × 250 m pixels (3 × 3 pixel grid) near each of the two blocks. Each area for EVI estimates was chosen based on its proximity and to include similar vegetation as the block. We then integrated the area under the curve for each hydrological year to get a proxy for cumulative EVI. The EVI anomaly is the deviation of this cumulative EVI in each hydrological year from the mean. We averaged EVI anomalies across pixels and across the two sites to visualize temporal trends.

Plant species composition and aboveground net primary productivity (ANPP)

Herbaceous richness (number of species/4 m^2) and evenness (E_{var}; Smith and Wilson 1996) were both calculated from plant species abundance data. From 2006 to 2017 (excluding 2015 and 2016), we surveyed herbaceous plant community composition near the beginning (January) and end (March) of each growing season to capture peak abundance of early and late-season species in four 1 × 1 m subplots within 2 × 2 m plots within each herbivore exclosure. We estimated the percent cover (to the nearest 1%) for each plant species rooted within each 1 × 1 m subplot and then cover estimates were averaged for each species across the four subplots for subsequent analyses at the plot level.

ANPP was collected at different locations within exclosures each year 2006–2014 and 2017 at the end of each growing season. Biomass from three 0.1-m^2 quadrats per exclosure was clipped at the soil surface and sorted into grass, forb, and previous year dead. Previous year dead was not utilized in these analyses. Current-year biomass was dried at 60°C for 48 h and weighed to estimate ANPP. Quadrat ANPP values were averaged by exclosure.

Statistical methods

Bray–Curtis dissimilarities from species abundance information were compared using permutational MANOVA to test whether plant communities differed among fire frequencies each year prior to the drought. These differences were visualized using nonmetric multidimensional scaling (NMDS), which collapses variation in the Bray–Curtis matrix down to two axes (in this case). Differences of total, grass, and forb ANPP among fire frequencies were assessed in two ways. First, repeated-measures ANOVA with block set as a random factor was used to assess differences in ANPP among pre- and postdrought time periods and fire frequencies for grass, forb, and total ANPP separately. Second, for visualization, response ratios were calculated for total, grass, and forb ANPP at the plot level by comparing predrought ANPP with postdrought ANPP:

$$\ln\left(\frac{\text{ANPP}_{\text{POST}}}{\text{ANPP}_{\text{PRE}}}\right)$$

where $\text{ANPP}_{\text{POST}}$ is the plot-level ANPP measured in 2017, and ANPP_{PRE} is the plot-level ANPP averaged across 2006–2014. Predrought ANPP values were averaged through time to gain a longer-term representation of predrought values than a single year. Whether 95% confidence intervals overlapped zero informed differences between postdrought and predrought. Forb : grass ratios were calculated for each fire treatment annually before (2006–2014) and after (2017) the drought.

Change in absolute abundance was calculated for each species at the plot level by subtracting the absolute percent cover postdrought in 2017 from average predrought abundance from 2006 to 2014. For each plot, we then selected the maximum and minimum cover difference within four categories of species (annual forbs, annual grasses, perennial forbs, and perennial grasses), binned these responses into 10% cover response categories, and calculated the proportion of plots from the total number of plots within each burn frequency that contained species responses within predetermined bins. Our aim with this analysis was to show which of the four species categories were declining most strongly, and which were contributing most to resilience of ANPP. We used maximum and minimum species responses instead of all species responses to avoid many small or null species differences swamping out species responses of greater magnitudes.

Species richness and evenness were calculated from species abundance data at the plot level. Species richness was estimated as the number of unique species within a plot in each year. E_{var} was used as an estimate of evenness, $–E_{\text{var}}$ is a measure of the variance in abundance values across all present species and is independent of richness.

Repeated-measures ANOVAs were produced using the MIXED procedure in SAS, version 9.4 (Cary, North Carolina, USA). All other calculations and analyses were done in R version 3.4.1 (R Core Development Core Team 2018). We used R packages to calculate SPI (*SPEI*; Vicente-Serrano et al. 2010), EVI integration (*pracma*; Borchers, 2018), richness, and E_{var} (*codyn*; Hallett et al. 2019), and to create NMDS plots (*vegan*; Oksanan et al. 2018).

Results

Precipitation in the 2015 hydrological year (359.2 mm) was well below the long-term site mean (547 mm/yr) and 2016 was the driest hydrologic year since 1937 (142.2 mm). This event was 1 of 10 "extremely dry" drought events from 1937 to 2017 and highlights a potential increase in drought severity at this site (Fig. 1A; Appendix S1: Fig. S2). The 2015/2016 drought had large impacts on vegetation (Appendix S1: Fig. S3), resulting in the lowest EVI recorded at our study site (MODIS data available from 2000 to 2017; Fig. 1C shows EVI anomalies averaged across both sites). Integrated EVI during the 2015 and 2016 hydrological years showed a 44 and 89% reduction, respectively, from the average integrated EVI during 2000–2014 at the N'wanetsi block. At the Satara block, integrated EVI showed a 43 and 83% reduction in 2015 and 2016, respectively. Precipitation in the 2017 hydrologic year was slightly above average at 638 mm (70th percentile), and average precipitation during the predrought period 2006–2014 was 585 mm (59th percentile).
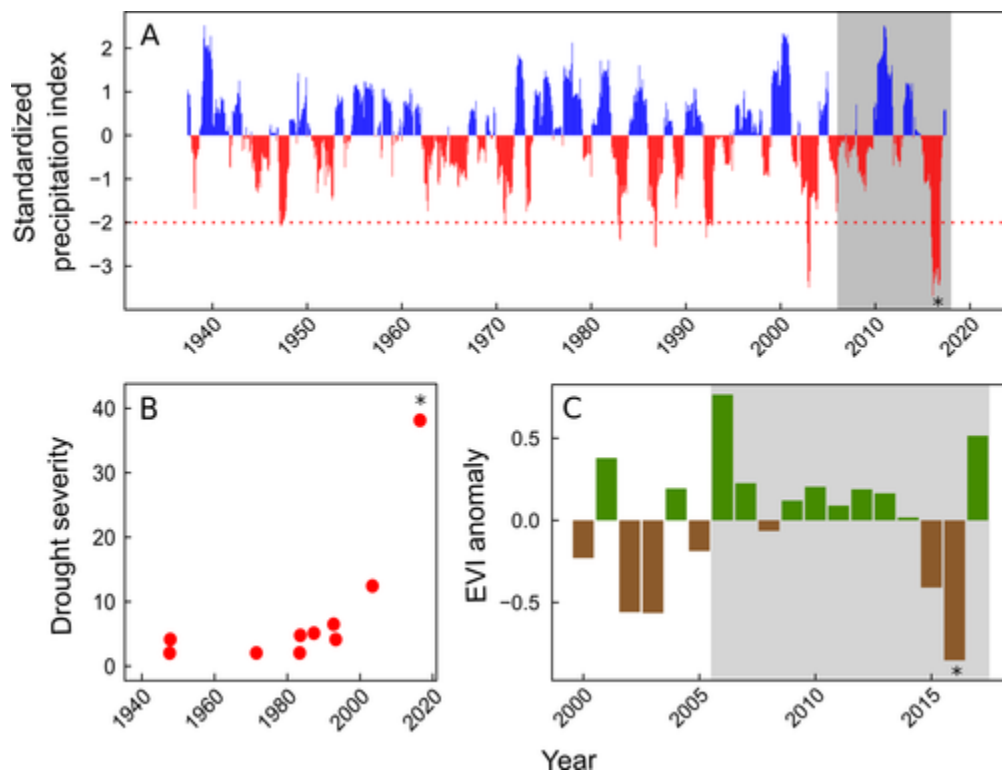

Figure 1. 2015/2016 Satara drought. (A) Twelve-month standardized precipitation index (SPI) for Satara, Kruger National Park, South Africa. Zero represents average precipitation and anomalies are represented as positive/blue and negative/red. Dotted line indicates "extremely dry" conditions (SPI <-2). (B) Drought severity trends for "extremely dry" events ($n = 10$) in the time series. For each of these events, the severity metric represents the summation of monthly SPI deviation from average (i.e., depth of red bar in panel (A)) for all successive months where SPI remains <-2. (C) Season-long integrated enhanced vegetation index anomalies from the 2000–2017 mean. This pattern shows the large-scale context of the drought impacts on season-long vegetation greenness that the experiment is nested within. Asterisk highlights the 2015/2016 drought year in all panels, shaded region in A and C show the study period.

Fire frequency effects on plant communities (predrought)

Permutational MANOVA analysis and NMDS showed significant differences in plant community composition between sites without fire and those burned at annual and triennial frequencies from 2006 to 2014. Differences between annually and triennially burned plant communities were less pronounced and transient, being significant in 2006 and 2009–2012 (Fig. 2A; Appendix S1: Tables S1–S3). From 2006 to 2014, annually and triennially burned areas tended to have fewer forb species and lower grass E_{var} compared to unburned areas (Fig. 2B–E).
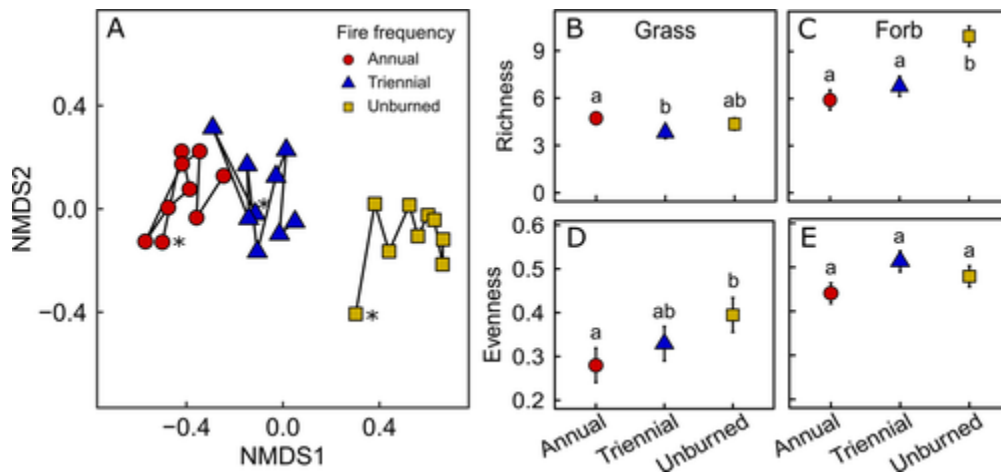

Figure 2. Predrought (2006–2014) differences of plant communities across different fire frequencies shown by (A) nonmetric multidimensional scaling (NMDS) ordination, (B) grass species richness (species per 4-m² plot), (C) forb species richness, (D) grass evenness, and (E) forb evenness. In (A), the points represent the mean scores across replicate plots each year, with the asterisk indicating 2006—the first year that measurements were taken. In (B–E), symbols represent richness and evenness, averaged across years. Error bars represent standard error, and different letters within panels represent significant differences among burn frequencies at $\alpha = 0.05$.

Resilience of total, grass, and forb ANPP

Across all three fire frequencies, total ANPP recovered to predrought levels during the 2017 growing season (Fig. 3A). This result parallels EVI trends, which also show full recovery in 2017 (Fig. 1C). In annual and triennial burns, grass ANPP was reduced by 49 and 59%, respectively, after the drought, whereas forb ANPP increased 309 and 340%, respectively (Fig. 3A; Appendix S1: Tables S4). In unburned areas, we observed no significant change in grass or forb ANPP postdrought (Fig. 3A, Appendix S1: Tables S4). During 2006–2014, we observed two major patterns of grass and forb ANPP: (1) grass and forb ANPP varied similarly by both increasing or decreasing in high- or low-productivity years, respectively (Fig. 3B, points falling along a positive relationship), or (2) low forb ANPP and high grass ANPP (Fig. 3B, bottom-right points). Immediately postdrought, this trend was reversed such that forb ANPP greatly increased, whereas grass ANPP decreased in annual and triennial burns (solid red and blue symbols, respectively, in Fig. 3A). This led to a forb-dominated ecosystem in 2017 (Fig. 3B, inset).
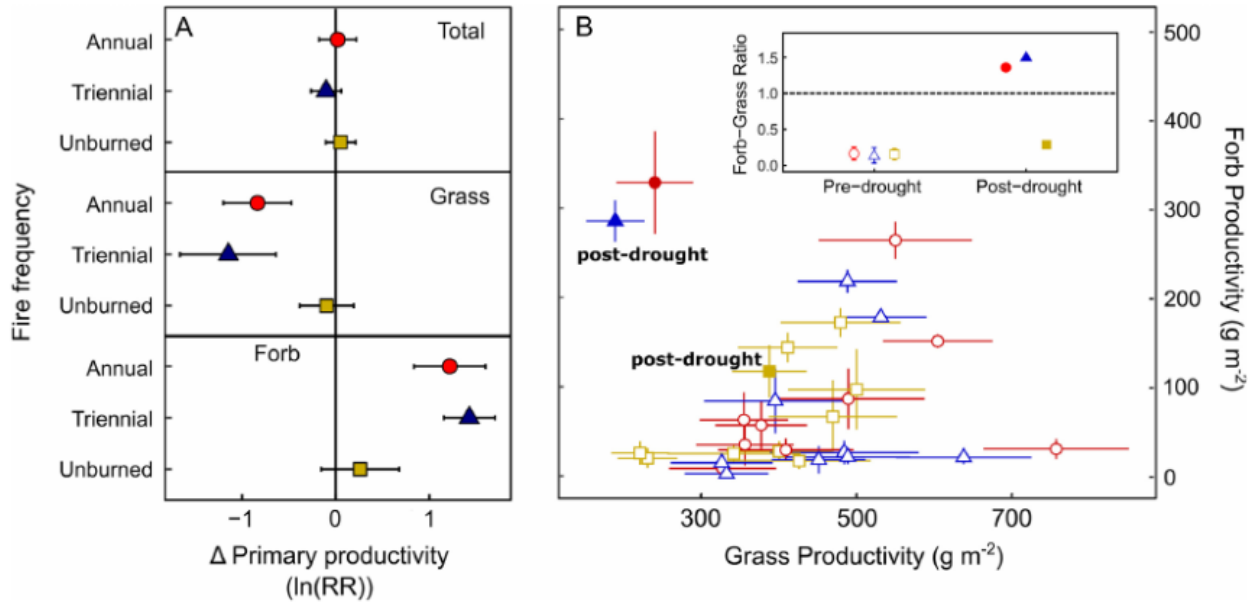
Figure 3. (A) Change in total, grass, and forb aboveground primary productivity from before to after the 2015/2016 drought under three different fire frequencies in Kruger National Park. Natural log-transformed response ratios were calculated at the plot level as ANPP postdrought divided by ANPP predrought; points represent the average response ratio across plots for each fire frequency. Predrought production values used were averages across 2006–2014, and postdrought productivity values were from 2017. Error bars in panel A represent 95% confidence intervals. (B) Relationships between grass and forb biomass in annual, triennial, and unburned fire treatments from 2006 to 2014 (open symbols) and 2017 (closed symbols). The inset shows forb:grass ratios before and after the drought. Note that values above the dotted line indicate a forb-dominated system, whereas values below the line represent grass dominance. Error bars in panel B represent standard error across replicates (main) or across years (inset).

Species-level responses

Certain perennial grass species declined across all three fire frequencies, with declines in absolute cover ranging from −40 to −100% cover (Fig. 4, bottom panels). The species most frequently making up these declines was *B. radicans*. The types of species that compensated for these declines (Fig. 4, top panels) varied depending on fire frequency. In annual and triennial burns, compensation was dominated by annual forb species (Fig. 4A, B top panels)— *Indigastrum parviflorum* often shifted from very low abundance to 100% absolute cover, and was the primary species representing the positive annual forb shifts shown in Fig. 4A, B. In unburned areas, compensation was driven by annual and perennial grass species (Fig. 4C top panel), including *Urochloa mosambicensis*, *Panicum coloratum*, and *Brachiaria deflexa*. Increases of annual and perennial grass species in unburned areas were typically more modest than in annual and triennial burns because predrought levels of these grasses were often high, limiting the absolute cover increase possible.
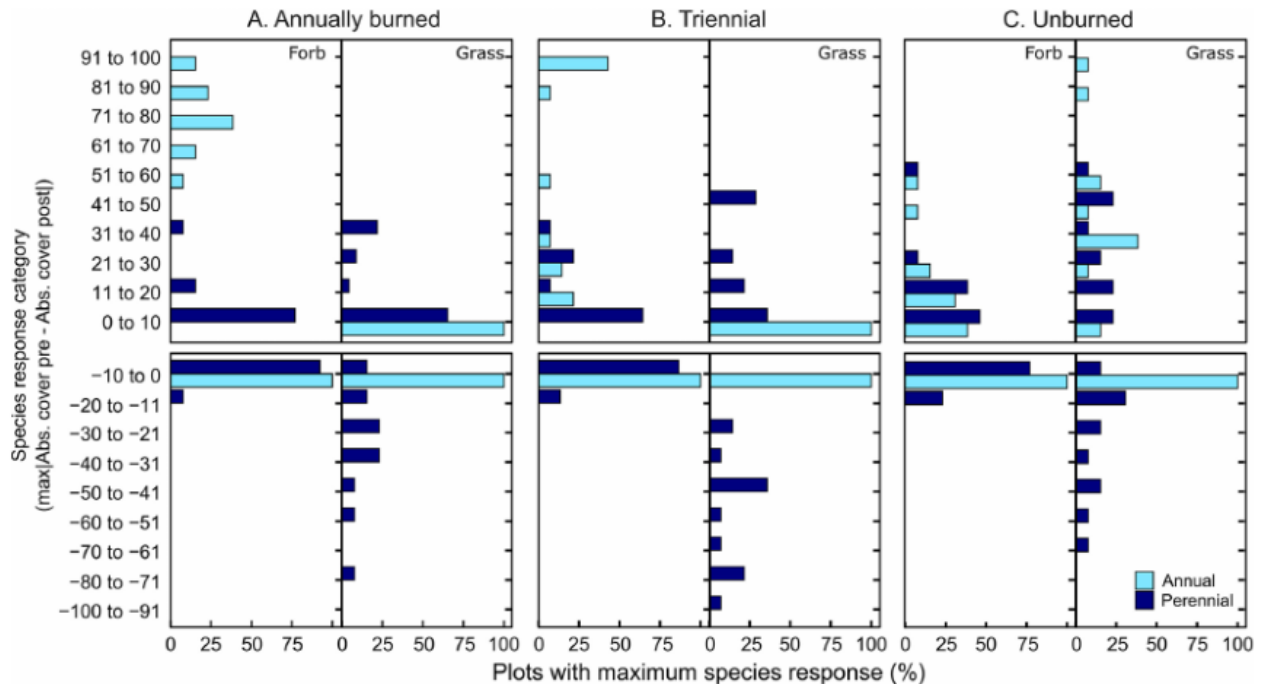
Figure 4. The percentage of plots exhibiting particular annual or perennial grass and forb species abundance changes in (A) annually burned, (B) triennially burned, or (C) unburned areas. Bars were calculated by first taking the maximum and minimum species response pre- vs. postdrought within each plot for each of four types of plant species: annual grasses, annual forbs, perennial grasses, and perennial forbs. As such, we show the major species that declined because of drought (bottom panels), and the major species that provided compensation for these declines (top panel). Species responses were then binned into 10% categories, and the number of plots having species responses falling within each bin were divided by the total number of plots. Species responses were determined by subtracting plot-level species absolute cover in 2017 from the plot-level species absolute cover averaged across 2006–2014. Only the most positive and most negative species shifts within annual forb, annual grass, perennial forb, and perennial grass categories were considered to avoid many small or no-change responses overwhelming signals of substantial species shifts.

Discussion

In this study, we addressed two major questions: First, what is the resilience of primary productivity after an exceptional drought? Second, what roles do grass and forb functional groups play in the resilience of the system? Overall, we found that ANPP was highly resilient to drought, returning to predrought levels in a single year. In frequently burned areas, rapid resilience was due to forbs (primarily annual) compensating for declines in grass ANPP. Alternately, in unburned areas, grass ANPP was highly resilient due to subdominant grass species compensating for declines in more common grass species (Fig. 4), and this may be linked to the evenness of grass species in these areas. These observations are consistent with emerging patterns that suggest grasslands have low resistance, but high resilience to drought (Ruijven and Berendse 2010, Stampfli et al. 2018, Stuart-Haëntjens et al. 2018). We posit that a better understanding of the various ways that compensation can occur is critical for understanding the capacity of grassland ecosystems to recover from extreme events.

Functional group compensation

Environmental fluctuations can affect grass and forb productivity in three ways (Appendix S1: Fig. S4). First, similar proportions of grasses and forbs could be altered by drought as well as during recovery, which would lead to a consistent ratio between forbs and grasses as environmental conditions vary (white band in Appendix S1: Fig. S4). Second, grasses may increase while forbs decrease, because of either compensation for losses in forbs or because of competitive impacts, such as light limitation, of grasses on forbs (yellow section). Third, forbs may increase while grasses decline, again because of compensation or competition (blue section). During years of nominal precipitation (2006–2014), grass–forb ratios exhibited patterns consistent with the first two scenarios: forb and grass ratios either remained relatively consistent (unburned points), or grass production increased at the expense of forb production (Fig. 3B, open symbols, frequently burned). The only time we observed forb compensation or competition effects on grasses was the year after the extreme drought in annual and triennial burned areas (Fig. 3B, filled symbols). This suggests that community responses and resilience mechanisms may differ strongly with nominal variation in precipitation vs. extreme droughts.

Postdrought compensatory dynamics are particularly important when drought results in individual mortality or loss of species. When mortality occurs, compensation may manifest as reduced density (abundance) or loss of drought-intolerant plant species along with increased abundance of those species that persist through drought or rapidly recover and expand after drought. This shift in abundances (i.e., density or mortality compensation, Gonzalez and Loreau 2009, Lloret and Escudero 2012) may be a primary mechanism of ecosystem resilience to drought. In this system under annual and triennial burn regimes, compensation was borne out via annual forbs likely expanding into vacated space created by the loss of the dominant grass, *B. radicans* (Fig. 4A, 4). Although compensation dynamics were only documented here within grazing exclosures because of logistical challenges associated with measuring ANPP in grazed areas, personal observations outside of exclosures in 2017 suggest that these dynamics are generalizable to grazed systems as well. Such patterns of compensation correspond with previous work in annual Californian grasslands showing exotic annual species displacing native vegetation after disturbance (HilleRisLambers et al. 2010). Functional compensation after extreme drought has also been shown in a U.S. tallgrass prairie, but in that system drought resilience was driven by increased grass ANPP compensating for mortality-driven declines in perennial forb ANPP (Hoover et al. 2014). The major difference between our study and Hoover et al. (2014) was that the drought in KNP resulted in substantial mortality of the dominant species, *B. radicans*, whereas the drought in tallgrass prairie resulted in little mortality of the dominant C_4 grass, *Andropogon gerardii*. Below, we discuss species-level patterns of responses to explore potential mechanisms behind compensation effects.

Intrafunctional group and species-level compensation

In all three fire frequency treatments, the dominant grass *B. radicans* was the primary species experiencing declines in abundance. In unburned areas, these declines were compensated by gains in abundance by annual and other perennial grass species. Numerous plots had grass species that gained 20–60% absolute cover postdrought and a few plots had annual grasses

increasing from near zero to ca. 100% (light blue bars at top of Fig. 4C). Forb species did not gain more than 20% absolute cover from predrought abundances in most unburned plots. In annual and triennially burned plots, *B. radicans* was largely replaced by an annual forb, *I. parviflorum,* which was present in the community but at low abundance. In unburned areas, *B. radicans* was primarily replaced by other grasses, such as *U. mosambicensis* (perennial–biennial), *P. coloratum* (perennial), and *B. deflexa* (annual)*,* which were already codominant (former two) or in lower abundance (latter) in the community. The lack of compensation by the annual forb *I. parviflorum* in unburned areas may be due to a thicker litter layer limiting the amount of light and space available for germination or persistence of this low-statured plant. Additionally, the thicker litter layer in unburned areas may be contributing to increased resilience of existing perennial grasses through retention of soil moisture during drought and less negative osmotic potentials (Knapp 1985) preventing complete mortality of belowground organs.

Species richness is predicted to have strong impacts on ecosystem resilience to drought (Tilman and Downing 1994) by increasing the likelihood of having species well poised to compensate for mortality of other species (Figge 2004). Yet, we found no evidence that greater grass or forb richness was related to greater resilience of total, grass, or forb ANPP (Figs. 2 and 3). Alternately, communities in unburned areas had higher grass evenness compared to frequently burned areas (Fig. 2), which coincided with high resilience of grass ANPP postdrought. As such, we suggest that resilience of the unburned community may be driven more by evenness than richness. This may be especially important for perennial systems under extreme drought, because propagation of many perennial grassland species is often via clonal reproduction (Benson and Hartnett 2006), which may limit compensation by species having initial low abundances within the community.

Conclusions

We observed substantial and consistent resilience of ANPP to extreme drought in a South African savanna grassland across three different fire frequencies, despite predrought differences in plant community composition. In the annually and triennially burned communities, declines in grass productivity were compensated by an increase in forb productivity. In contrast, there was little observed change in the productivity of these functional groups in the unburned community. However, across all fire frequencies, *B. radicans*, a dominant or codominant grass prior to the drought, declined and was either replaced by an annual forb (annual/triennial burn), an annual grass (some areas in unburned), or multiple codominant grasses (most of unburned).

There are several important implications of these results. First, resilience at the ecosystem level (e.g., total ANPP) may not mean resilience at the community level (e.g., individual species or plant functional groups). Although stability in total ANPP is important for ecosystem services such as carbon storage, changes in the ratio of grasses and forbs may affect forage quality and quantity for herbivores, as well as pollinator resources. Second, fire, which is known to be a major driver of ecosystem dynamics in grasslands (Pausas and Bond 2019), can strongly influence the compensation mechanism underlying drought recovery. Often, climate and soil are considered the primary drivers of ecosystem response to environmental drivers. Yet, based on our findings here, we suggest that fire, and its impacts on community structure, may be just as important in determining savanna-grassland dynamics. Finally, all three community types

exhibited resilience in ANPP despite predrought differences in plant composition. This suggests, along with other studies (Ruijven and Berendse 2010, Hoover et al. 2014, Stampfli et al. 2018, Stuart-Haëntjens et al. 2018), that grasslands across a broad range of disturbance regimes (and community dynamics) may exhibit rapid resilience after extreme drought. This resilience will be critical for long-term sustainability of grassland function and services.

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