

## RESEARCH ARTICLE

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# Grazer movements exacerbate grass declines during drought in an African savanna

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## Abstract

1. Rainfall variability, including drought, consistently translates into variation in grass productivity in savanna ecosystems. These variations in grass availability can impact grazer populations, which can in turn shape grass responses to drought.
2. However, despite clear evidence that grazers move freely in response to forage and water availability, drought ecologists have mostly failed to consider how these landscape-scale processes influence vegetation responses to drought.
3. Here, we ask how rainfall variability and drought, in interaction with population dynamics and movement of large grazers, shape grass layer responses in extant savanna landscapes in Kruger National Park in South Africa.
4. We found that grass biomass was highly responsive to rainfall variability; notably, grass declines during drought were especially severe—even more severe than previously documented elsewhere.
5. Grazing probably contributed, exacerbating drought effects in droughted regions and spatially extending them into non-droughted refugia, where grass biomass also declined. Moreover, the existence of these refugia potentially prevented a grazer population crash.
6. *Synthesis.* Our current focus on the physiological effects of drought is probably insufficient for understanding vegetation responses to drought. A renewed focus on landscape processes, including animal movement, will be critical to predicting savanna responses to increasingly frequent extreme events.

## KEYWORDS

climate extremes, drought, drought refugia, grass, grazer, migration, movement, savanna

## 1 | INTRODUCTION

Increasing rainfall variability—including variation in rainfall among years—is consistently predicted to be a major feature of climate change in the tropics and subtropics (IPCC, 2013; Rajah et al., 2014; Westra, Alexander, & Zwiers, 2013). Extremely high annual rainfall may be one feature of this, but concern often focuses on droughts and their effects on human and natural systems (Anderegg, Kane, & Anderegg, 2013; Knapp et al., 2008; Phillips et al., 2009; Smith,

2011). For instance, southern Africa has recently experienced a major 2-year drought, resulting in unprecedented water shortages in some areas. These droughts have major and potentially exceptional impacts on the grassy ecosystems that dominate the region.

Of course, grass itself responds directly rainfall variability, which has been examined extensively in observational and experimental contexts, with some specific emphasis on extreme drought. Rainfall variability appears consistently to translate into variation in grass productivity (Govender, Trollope, & Van Wilgen, 2006; Higgins,

Bond, & Trollope, 2000; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012; Staver, Botha, & Hedin, 2017; Wilcox et al., 2017). However, grass varies less in response to temporal variation in rainfall than to spatial variation in rainfall (Sala et al., 2012), because wet-to-normal years before droughts subsidize productivity, while dry-to-normal years before high rainfall extremes can carry over to suppress it. These so-called legacy effects lead to lagged grass responses to rainfall variability. Proposed mechanisms include changes in stored labile carbon and tiller production and mortality dynamics (Reichmann, Sala, & Peters, 2013). The net effect is that grass productivity and biomass respond but may be relatively resistant to drought (Byrne, Adler, & Lauenroth, 2016; Frank, 2006; Hoover, Knapp, & Smith, 2014), perhaps even more resistant to drought than to exceptionally high rainfall (Wilcox et al., 2017).

Reductions in grass biomass and productivity during drought, even muted ones, nonetheless translate into substantial forage limitation for grazers in savannas, and grazers in turn can amplify grass responses to drought. Large-scale analyses suggest that droughts can cause major, even massive, declines in herbivore population numbers under some circumstances (Augustine, 2010; Ogutu & Owen-Smith, 2003; Walker, Emslie, Owen-Smith, & Scholes, 1987; Young, 1994), resulting from some combination of forage limitation (Augustine, 2010; Illius & O'Connor, 2000) and direct access to water (Redfern, Grant, Gaylard, & Getz, 2005; Smit, Grant, & Devereux, 2007). These major declines are seemingly at odds with drought experiments showing that grass biomass and productivity are relatively resistant to drought, but may result from grazers themselves exacerbating grass biomass declines during droughts. Grazing mammals certainly affect grass biomass and productivity during normal rainfall conditions in systems ranging from North American prairie (Koerner & Collins, 2014) to the Serengeti (Holdo et al., 2009) to South African savannas (van der Plas, Howison, Mpanza, Crooms, & Olf, 2016; Staver & Bond, 2014) and beyond. To a more limited extent, exclusion experiments have also suggested that grazing can interact with drought to intensify grass responses to drought (Donaldson et al., 2017; Porensky, Wittman, Riginos, & Young, 2013), but results are inconsistent (Koerner & Collins, 2014) and have yet to be generalized.

To compound this, we rarely think about how these grazer-drought interactions play out in the landscape context for vegetation, despite extensive evidence that herbivores move dramatically in response to forage and water availability, both during normal years (Anderson et al., 2010; Hopcraft, Olf, & Sinclair, 2010; McNaughton, 1990) and during droughts (Ogutu & Owen-Smith, 2003; Augustine, 2010). In rangeland contexts, large-scale movements of livestock (usually by people) in response to rainfall variability are routine (Butt, Shortridge, & WinklerPrins, 2009; Campbell, 1999; Ngugi & Conant, 2008). However, this perspective is rarely extended to explicitly consider how this might affect vegetation responses to drought (but see Augustine & McNaughton, 2006), and most of what we know about drought effects on savanna vegetation comes from localized experimental or observational physiological work. Even herbivory experiments, while slightly larger (ranging from a few square

metres to hectares at most), have also been necessarily relatively restricted compared to the landscape scale at which animals move. These animal movements in a spatially heterogeneous drought could have major impacts on grass responses to drought, and feed back onto grazer population dynamics in turn (Augustine, 2010; Illius & O'Connor, 1999; Ngugi & Conant, 2008).

Here, we ask how rainfall variability, including drought, drives variability in the grass biomass in a large conservation area in South Africa savanna (Kruger National Park), in interaction with movement and population dynamics of large grazers. Droughts are of particular interest in South Africa, because droughts in South Africa are increasingly associated with major El Niño events (Faucherau, Trzaska, Rouault, & Richard, 2003), the incidence of which is increasing (Cai et al., 2014). Responses of the grass layer, especially as they affect sensitive grazer populations, are of increasing ecological interest and of major conservation concern, which demands that we move beyond small-scale experimental evaluations of drought towards a larger scale landscape perspective.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Kruger covers nearly 20,000 km<sup>2</sup> (22°20' to 25°30' S; 31°10' to 32°00' E) in low-elevation areas (260 m–839 m; the “lowveld”) of northeastern South Africa. It is dominated by two underlying geologic substrates, a granite and a basalt, broadly characterized as sandy, nutrient-poor versus clayey, nutrient-rich soils respectively (Staver et al., 2017). The flora of Kruger includes 400+ species of tree and shrub and 200+ species of grass, including most commonly *Urochloa mosambicensis*, *Digitaria eriantha*, *Panicum maximum*, and *Bothriochloa radicans*. Mean annual rainfall ranges from 350 mm to 750 mm, although interannual variation is significant. Since 1960, park management has continuously maintained 22 daily rainfall measurement stations throughout the park, from which spatially explicit rainfall surfaces are generated via inverse distance weighting, and one daily temperature measurement station.

The park is also host to a diverse assemblage of African mammals, including large populations of elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), and impala (*Aepyceros melampus*). Spatially explicit herbivore population data are available only for elephants and buffalo from fixed-wing aerial population censuses (annual during June–July from 1985 to 2012 and again in 2015 and 2017) and, of these, buffalo contribute a significant fraction of grass consumption among herbivores in the park. Finally, fire maps maintained by park management were used to examine whether fire occurrence before drought onset covaried with subsequent drought severity.

### 2.2 | Grass biomass data

Kruger management established 533 Veld Condition Assessment (VCA) sites (198 on granitic and 165 on basaltic soils, with the others on less prominent geologic formations) to monitor grass

biomass to inform fire management, starting in 1989 (see Staver et al., 2017; Staver, 2018 for more information). Grass biomass was measured every year in March–April in plots of 50 m × 60 m with a calibrated disc pasture meter. Measurements to derive plot-level grass biomass estimates were taken every 2 m along four 50-m transects, running at 0 m, 20 m, 40 m, and 60 m along the length of the plot (for a total of 204 disc pasture meter readings per plot to establish average plot-level grass biomass). Grass was measured annually from 1989 until 2012 and again in 2016 and 2017, but the subset of plots that were actually sampled every year varied substantially in number and identity (a minimum of 108 sites were sampled in 2007 and a maximum of 532 in 1995; 25th percentile = 370; 75th percentile = 503).

Kruger also has a history of water provisioning at artificial waterpoints (including dams and pumps), which could potentially affect animal distributions and therefore vegetation structure (Redfern et al., 2005). Unfortunately, the park has not maintained a consistent record of waterpoint distribution through time, such that analysis of the effects of water provision on grass is impossible across the entire grass dataset. The park's management planning suggests that artificial waterpoint provisioning reached its peak in the early 1990s, when concerns about overstocking of “water-dependent” species led to rolling waterpoint closures throughout the 1990s and 2000s (Ogutu & Smith, 2003; Redfern et al., 2005). The location and status (open vs. closed) of all waterpoints was evaluated in 2011 and again in 2016, however, such that we have been able to evaluate the effect of distance from active waterpoints on grass biomass during the 1992 and 2016 droughts. These analyses are included in the Supplements; results suggest no qualitative differences between 1992 and 2016, such that trends in water provisioning likely do not provide an explanation for the patterns presented in the main body of the paper.

## 2.3 | Data analysis

We analysed data (1) to examine interannual variation in grass biomass with respect to “normal” variation in rainfall and temperature, in interaction with soils, (2) to determine whether grass responses to extremes were consistent with grass variation during normal years, and (3) for insight into why extreme droughts might differ qualitatively from “normal” grass biomass variation, to evaluate how two separate extreme droughts (in 1992 and 2014–2016) differed

in their effects on grass biomass and herbivore landscape distributions. Here, we have used a standard definition for extreme rainfall, in which an extreme year has rainfall that differs from the mean by >40% (see Knapp, Hoover, et al., 2015). This definition yielded two droughts, one during the 1991–1992 growing season and another 2-year drought during the 2014–2016 growing seasons, and one exceptionally high rainfall year during the 1999–2000 growing season (with an impressive >200% of normal rainfall across the park).

For (1), we fit linear mixed-effect models using observed plot-level data from all “normal” years, defined as those with non-extreme rainfall and not immediately following extreme years (i.e., including all data except that collected during 1992–1993, 2000–2001, and 2016–2017). Grass biomass was modelled as the response variable, with rainfall, previous-year rainfall, temperature, year, and geologic substrate as fixed effects and plot identity as a random effect. We also considered possible interactions between rainfall and geologic substrate (because soil texture has been proposed to mediate rainfall availability; e.g., Case & Staver, 2018) and between rainfall and previous-year rainfall (because these have been proposed to interact; see Sala et al., 2012). Thus, the most complicated possible model is given by

$$\begin{aligned} \text{grass biomass} &\sim \text{rainfall} + \text{previous-year} \\ &\text{rainfall} + \text{substrate} + \text{temperature} + \text{year} + \text{rainfall} \times \\ &\text{substrate} + \text{rainfall} \times \text{previous-year rainfall} + (\text{random effect} = \text{site}) \end{aligned}$$

Models were compared using AICc (see Table 1 for results).

For (2), we fitted a model that did not include rainfall lag as a factor, which allowed us to calculate deviations, during and following extreme events, from the “standard” model for grass response to rainfall and temperature variation, and thus to evaluate the rate of recovery of the grass layer from these major events. These deviations were evaluated via the residuals of model predictions across all years (fit only to non-extreme years, but used to predict extreme years as well as normal ones). The structure of this model and its fit statistics are given in Table 1.

To compare ecological effects of two extreme droughts (Aim [3]), we analysed grass biomass and buffalo landscape use responses to drought in 1992 versus 2016 in separate linear models. As above, grass biomass responses to rainfall were modelled at the plot level; here, we calculated mean grass biomass across all non-extreme

Model	$\Delta\text{AIC}_c$	Variation explained
grass ~ rain × substrate + rain lag + year + temperature	0	60.5%
grass ~ rain × substrate + rain × rain lag + year + temperature	2.67	60.6%
grass ~ rain × substrate + rain lag + temperature	13.47	60.4%
grass ~ rain × substrate + temperature + year	263.0 <sup>a</sup>	59.3%

<sup>a</sup>Note that this is not the fourth best model overall, but was used to generate predictions and residuals for Figure 2.

**TABLE 1** Model AIC<sub>c</sub> for grass biomass prediction. We list only the three best models, as well as statistics for an additional model used to generate results for Figure 2. Here again, data were included only for years that were not extreme and that did not follow extreme years. All models controlled for plot as a random effect

years for each plot and then calculated the grass biomass drought-anomaly as a proportional change during the drought year (i.e., proportional  $\Delta$  biomass = [mean biomass – drought biomass]/mean biomass). Buffalo densities were calculated from census locations by rasterizing to a 20-km grid for comparison through time, then averaged to create mean buffalo density maps; buffalo density drought-anomalies were calculated across the park (as  $\Delta$  density = mean density – drought density; note that the high incidence of zeros in these data made the use of proportional change statistics impractical). To ensure that we were considering the buffalo movements that actually shaped grass biomass responses, we extracted and analysed buffalo anomalies at each grass biomass monitoring site that was actually sampled during the drought in question (either 1991–1992 or 2014–2016) for analysis. Note that because buffalo were not censused in 2016, we used 2017 census data as a best-estimate to represent the cumulative effects of 2 years of drought on buffalo distributions. Proportional rainfall anomalies were calculated via the same method as proportional grass biomass anomalies.

All spatial data manipulation, statistics, and figure preparation were done in R, version 3.2.2, using the packages “gstat,” “lme4,” “maptools,” “MuMIn,” “raster,” “rgdal,” “rgeos,” and “sp.”

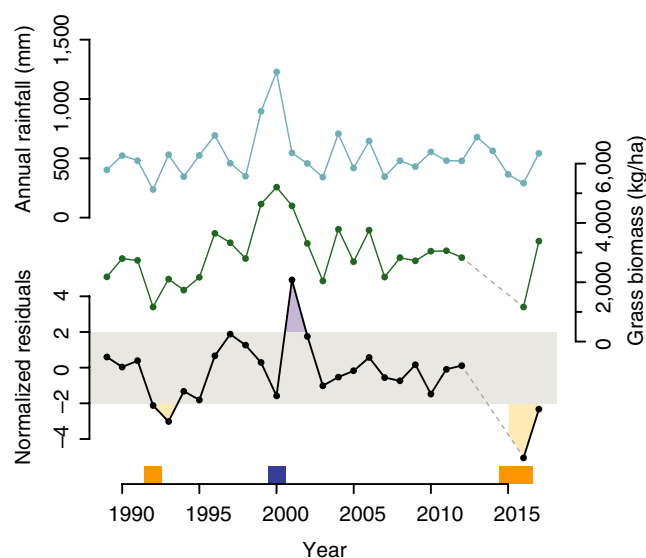
### 3 | RESULTS

During normal years (i.e., not during or immediately following high or low rainfall extremes), grass biomass increased with annual rainfall (Figure 1a) and previous-year rainfall (Figure 1b), in interaction with geologic substrate (more grass on clay- and nutrient-rich basalts vs. granites; see also Staver et al., 2017) (see Table 1). Higher temperature was also associated with lower grass biomass; and despite a temperature increase of 0.85°C from 1960 to 2009 (a rate of warming consistent with changes in global mean surface temperature; Hansen et al., 2006), grass biomass also increased slightly through time (see Table 1).

Qualitatively, grass responses to rainfall during extreme years were consistent with responses during normal years: grass biomass increased during exceptionally high rainfall events and decreased during droughts. However, quantitatively, while the effects of exceptionally high rainfall (2000–2001) on grass biomass were reasonably well-predicted by the standard model, the lagged effects of high rainfall on grass biomass were exceptionally strong in the year following (2001–2002; see Figure 2). The effects of drought were even more

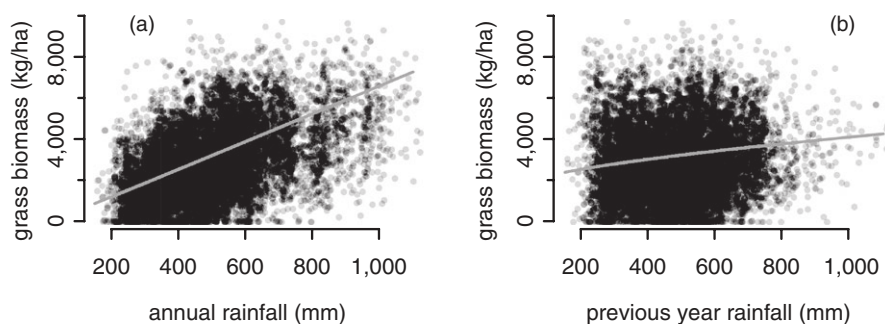
extreme; grass biomass decreased even more during drought years than predicted from their low rainfall, and these effects lasted into the year following drought (see Figure 2). These effects of drought were somewhat evident during 1991–1992, but were especially pronounced during the 2014–2016 drought, a difference that requires explanation.

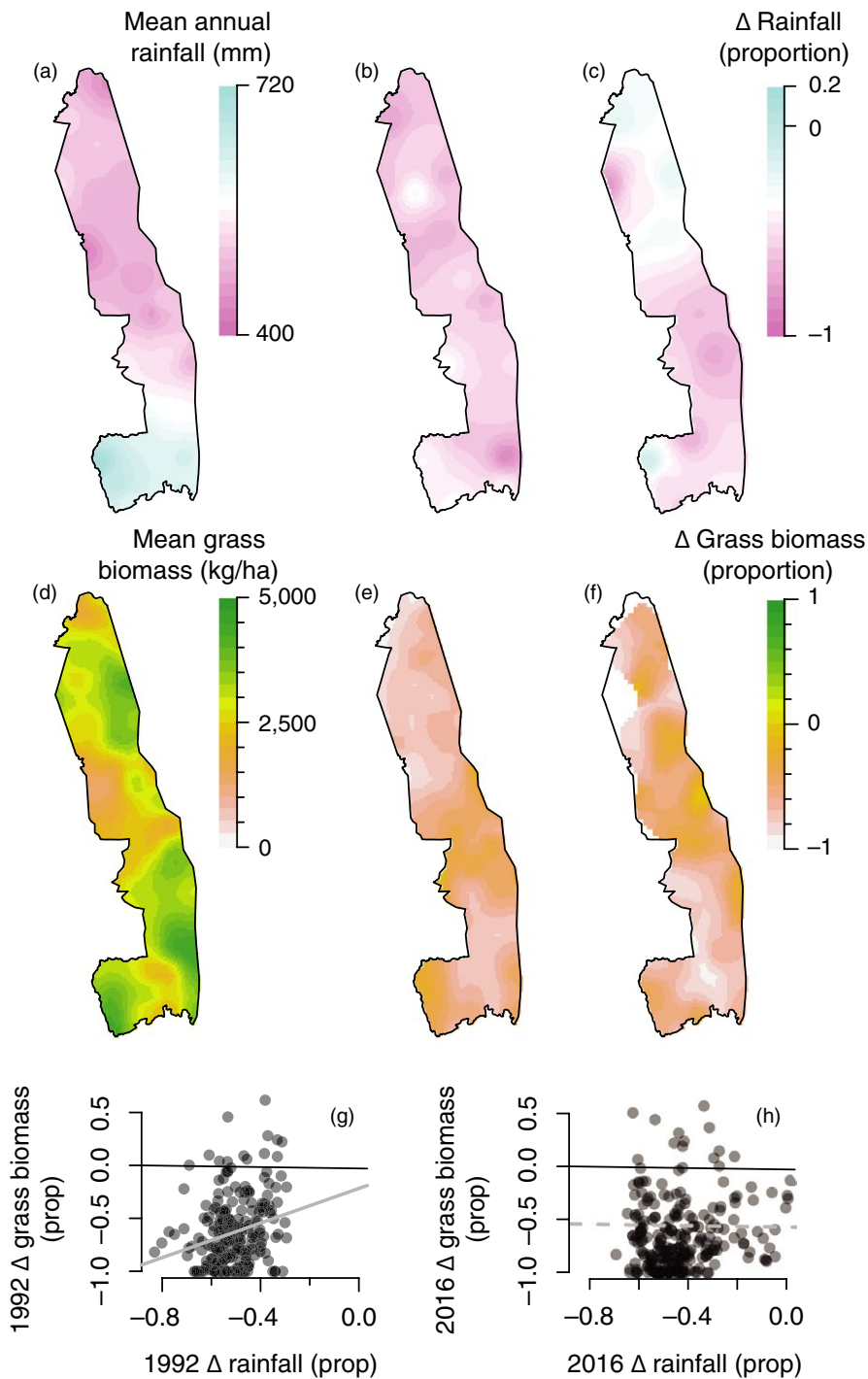
Most notably, although 1991–1992 and 2014–2016 experienced drought that was comparable in severity in some places, drought was much more uniform in 1991–1992 than it was in 2014–2016, when the entire north and southwest regions of Kruger experienced approximately average rainfall (see Figure 3a–c). However, curiously, average rainfall did not translate into average grass biomass in regions that did not experience drought in 2014–2016; reductions in grass biomass



**FIGURE 2** Rainfall (top), grass biomass (middle), and grass biomass residuals through time (bottom). To generate residuals, grass biomass was modelled via mixed effect models using year, temperature, and current year rainfall in interaction with substrate as fixed predictors, excluding observed grass biomass during exceptionally high and low rainfall years (high rainfall extremes highlighted in blue, droughts in yellow) (see Table 1). Grass biomass was unusually low during droughts and the year following; by contrast, exceptionally high rainfall effects were consistent with standard effects during the event itself, but persisted into the subsequent year resulting in unusually high grass biomass. The grey bar represents 2 standard deviations from the mean of normalized residuals (i.e., 95% confidence interval)

**FIGURE 1** Annual rainfall (a) and previous-year annual rainfall (b) versus grass biomass in Kruger during non-extreme years. Grass biomass increases significantly with both; fits are estimated from linear mixed-effect models (see Table 1 for statistical results)



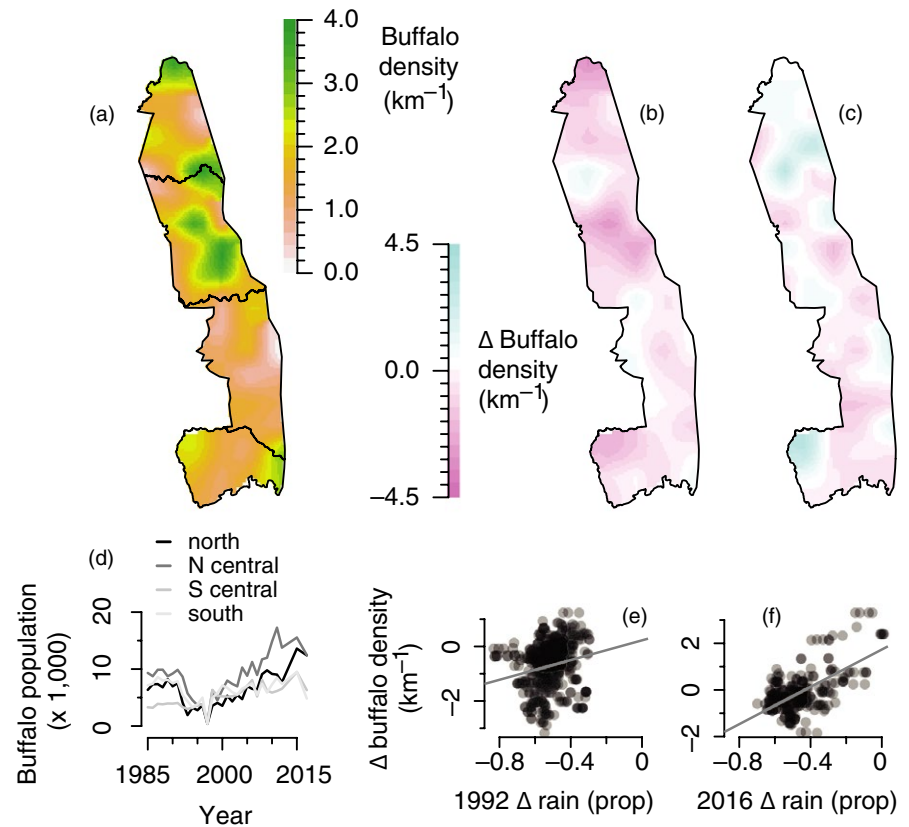


**FIGURE 3** Maps of mean annual rainfall (a), drought rainfall anomalies in 1992 (b) and 2016 (c), mean grass biomass (d), and drought grass biomass anomalies in 1992 (e) and 2016 (f); rainfall anomaly versus grass biomass anomaly in 1992 (g) and 2016 (h). Drought was more heterogeneous in 2016 than in 1992, but this was not mirrored in grass biomass responses, which were substantial even where drought was less severe. Note that for display only (d-f), plot-level observations of grass biomass and anomalies were interpolated via inverse distance weighting; however, all analyses were conducted on plot-level data without interpolation

were as widespread in 2014–2016 (Figure 3f) as they were in 1991–1992 (Figure 3e), despite drought effects that were more restricted. Moreover, while local drought severity weakly predicted the extent of the grass biomass anomaly in 1992 ( $R^2 = 0.065$ ,  $df = 223$ ,  $p < 0.001$ ; Figure 3g), grass biomass reductions were not related to localized drought severity in 2016 ( $R^2 = 0.007$ ,  $df = 222$ ,  $p = 0.22$ ; Figure 3h), despite the fact that drought was much more heterogeneous in 2014–2016 than it was in 1991–1992, which additional spread should have resulted in improved prediction. Instead, even regions that had normal rainfall experienced severe reductions in grass biomass (Figure 3h).

Rather than impacting standing grass biomass, heterogeneity in drought severity in 2014–2016 instead impacted anomalies in the spatial distribution of grazer distributions across Kruger ( $R^2 = 0.383$ ,  $df = 224$ ,  $p < 0.001$ ; Figure 4c,f). In 2014–2016, buffalo migrated to drought refugia and stayed there. By contrast, in 1991–1992, changes in grazer distributions were less related to drought severity ( $R^2 = 0.043$ ,  $df = 223$ ,  $p < 0.001$ ; Figure 4b,e), probably because drought did not vary in severity much within the park; instead, buffalo experienced widespread mortality (Figure 4d). Migration of buffalo to drought refugia may have helped mitigate mortality during 2014–2016, which in





**FIGURE 4** Maps of buffalo density (a) and buffalo density anomaly in 1992 (b) and 2017 (c); buffalo population trends through time (d); rainfall anomaly versus buffalo density anomaly in 1992 (e) and 2017 (f). Kruger's buffalo population crashed during the 1992 drought, but instead moved north to drought refugia during and after the 2014–2016 drought, which prevented widespread mortality, especially within drought refugia

turn changed and homogenized grass biomass reductions in response to localized drought.

Note that the occurrence of fire at a site before drought onset somewhat increased buffalo densities in both 1992 and 2016, consistent with a sizeable literature suggesting that fire scars can attract grazers due to a combination of forage quality and predator avoidance (Eby & Ritchie, 2012; Riginos, 2014). However, adding fire as an independent variable to models only marginally improved predictions of buffalo distributions in both years (1992:  $R^2 = 0.389$  over  $R^2 = 0.385$ ; 2016:  $R^2 = 0.389$  over  $R^2 = 0.385$ ). Drought severity did not differ between regions that experienced fire before drought onset versus those that did not, either (1992:  $R^2 < 0.01$ ,  $df = 494$ ,  $p = 0.15$ ; 2016:  $R^2 < 0.01$ ,  $df = 232$ ,  $p = 0.24$ ), such that herbivore movements in response to rainfall anomalies are not likely to have been caused by fire as a hidden variable covarying with drought severity (see Table S1 for full statistical results).

Accounting for distance to water and the potential effects of artificial water provisioning on grass biomass did suggest that, while distance to water affected grass biomass overall and distance to water increased between 1992 and 2016, it did not interact with or change the response of grass biomass to rainfall or buffalo density during drought (see Figure S1).

## 4 | DISCUSSION

Here, we found (1) that grass biomass was highly responsive to climate variability, especially rainfall, and (2) that recovery from

extreme events occurred on the time-scale of years, not decades. Notably, (3) grass declines during drought were especially severe—even more so than previously documented elsewhere, perhaps because (4) grazing dramatically reduced grass biomass during drought, even in parts of the landscape that experienced less severe drought. Large-scale animal movement to these drought refugia may have (5) spatially extended the effects of drought and (6) mitigated grazer mortality, preventing drought-driven population crashes.

That rainfall increases grass biomass and productivity is well known from a diversity of grassy systems (Knapp & Smith, 2001; Sala et al., 2012; Wilcox et al., 2017), including Kruger (Staver et al., 2017). Consistently across systems, spatial variation in mean annual rainfall determines spatial variation in grass biomass and productivity (Sala et al., 2012). Similarly, temporal variation in rainfall determines temporal variation in grass productivity, although legacy effects of previous years' rainfall can dampen variation in productivity through time (Knapp & Smith, 2001; Wilcox et al., 2017) because variability subsidizes productivity during dry years and suppresses productivity during wet ones (Oesterheld, Loreti, Semmartin, & Sala, 2001; Sala et al., 2012). Here, both normal and high rainfall years conformed to this expected pattern: rainfall lags were significant in predicting temporal variation in grass biomass under approximately average conditions (see Table 1; Figures 1,2), and an exceptionally wet year did not have exceptionally high grass biomass but did result in persistent increases in biomass, consistent with legacy effects lasting one or more years. Previous work suggests that legacy effects probably contribute, but patterns may also partly result from

our measuring standing biomass not productivity (which may carry over directly from one year to the next) and rainfall not soil moisture (thereby failing to account for runoff, which may be greater during high rainfall events).

However, grass biomass had an immediate and dramatic negative response to drought (in 1991–1992 and much more strongly so in 2014–2016), completely out of proportion with usual grass biomass responses to rainfall variability (see Figure 2). Experimental and observational work has repeatedly shown that the temporal effects of rainfall variability should be damped (Knapp & Smith, 2001; Sala et al., 2012), and that even severe droughts do not usually cause the magnitude of declines in grass biomass that we have observed here (Hoover et al., 2014; Knapp, Carroll, et al., 2015; Wilcox et al., 2017). One possibility is that these droughts have been exceptionally severe, exceeding the tolerance of the grass layer. However, we have documented two droughts within 30 years, and comparable droughts occurred in South Africa in the 1960s and 1970s, suggesting that these droughts were not exceptional for this system and may not fit the definition of true extreme events (Knapp et al., 2008; Knapp, Hoover, et al., 2015); moreover, recovery appears to be occurring on a time-scale of years, suggesting that grass biomass actually was relatively resilient to droughts of this magnitude (Hoover et al., 2014). Even so, further direct experimental evaluations of grass response and recovery from experimental drought might clarify the direct physiological impact of drought in this system.

A curious feature of the heterogeneous 2014–2016 drought suggests an alternative possibility: we found that buffalo populations moved to those areas of Kruger that did not experience drought (the north and southwest, where rainfall was approximately normal; see Figure 4), and moreover that grass biomass was abnormally low even in those regions that received average rainfall (Figure 3h). That grazers can move substantially during drought to supplement their forage is well known from grazing and especially pastoral systems (Augustine & McNaughton, 2006; Butt et al., 2009; Campbell, 1999), but our results suggest that these refugee populations of grazers had a fundamental role in determining vegetation responses to drought, which is often overlooked by ecologists interested in drought effects on vegetation (but see Augustine & McNaughton, 2006). At the most basic level, the co-occurrence of grazer population shifts and major unexpected reductions in grass biomass suggests that grazers may play a critical role in amplifying drought effects on grass biomass, driving immediate, large reductions in grass biomass that are not buffered by normal rainfall in preceding years.

Homogeneous reductions in grass biomass across the landscape, despite a heterogeneous drought, also suggest that grazers can extend the effects of drought beyond its strict geographic limits. While grazers can reinforce existing landscape heterogeneity during normal years (Archibald, Bond, Stock, & Fairbanks, 2005; McNaughton, 1984), forage limitation may reverse those effects during dry years, as grazers utilize both more and less preferred parts of the landscape. This phenomenon is consistent with previous work showing that browsers heavily utilize preferred sites during “good” years, but venture into less preferred sites during “bad” ones, distributing

browser impacts more broadly in the landscape (Riginos, 2014). By the same token, subsidies to herbivore diets from “source” environments can substantially amplify herbivore impacts into landscape “sinks” during times of scarcity (Illius & O'Connor, 2000), as e.g., in the Serengeti wildebeest and zebra migration (Anderson et al., 2010; McNaughton, 1990). Thus, drought may reverse the net effect of herbivory from creating patchiness during normal years (de Knegt, Groen, Vijver, Prins, & Langevelde, 2008; Riginos, 2014; Wilmshurst, Fryxell, & Bergman, 2000) to homogenizing an otherwise patchy environment during limited ones.

Movement at the landscape level by buffalo in response to heterogeneous drought appeared to have implications for buffalo population outcomes overall, as well. We observed that, during the more homogeneous 1991–1992 drought, 48% of the buffalo in Kruger died, whereas mortality was lower (25%) in response to the more heterogeneous 2014–2016 drought despite much higher overall population numbers (see Figure 4d). Note that some water-points were closed between 1992 and 2016, which may also have contributed to differing population-level responses (Redfern et al., 2005). Nonetheless, the existence of drought refugia in 2014–2016 may have acted as a key resource (Illius & O'Connor, 2000), allowing movement in response to drought, buffering buffalo against a major population crash, and preventing longer term changes in the ecology of this savanna. Thus, spatial processes spatially expanded the effects of drought but potentially prevented grazer population collapse, consistent with theoretical work suggesting that spatial processes can increase the resilience of diverse ecosystems (Villa Martín, Bonachela, Levin, & Muñoz, 2015).

Crucially, heterogeneity in drought severity could buffer Kruger buffalo against population crashes because Kruger is large and, at least in one instance, spanned variability in drought severity (see Figure 3c). Smaller reserves and rangelands should not necessarily expect grazer populations to be as resilient in the face of major droughts (Augustine, 2010), and fences even in large reserves like Kruger sometimes prevent grazers migrating to refugia (as in 1991–92). Historical accounts suggest that, before Kruger was fenced, animals migrated from the South African highveld to the Mozambican coastal plain, a route that has since been fenced with possible associated crashes in populations (Whyte & Joubert, 1988). Implications extend beyond South Africa. For one, we may need to consider how historical populations of large migratory grazers (e.g., North American bison; see Harris, Thirgood, Hopcraft, Croomsight, & Berger, 2009) may have altered the drought ecology of grasslands and savannas world-wide. More immediately, the few remaining great migrations in the world (most notably of zebra and wildebeest in the Serengeti) may suffer from the construction of barriers (Dobson et al., 2010), in drought years even more so than normal ones.

## 5 | CONCLUSIONS

Grass biomass responded as expected to rainfall variability, consistent with comprehensive previous work. However, drought

caused disproportionate declines in grass biomass, even in areas of the Kruger landscape that did not experience significant drought. Patterns of grazer movement suggest that intense grazing was likely responsible (see also Augustine & McNaughton, 2006), both for intensifying drought impacts and for homogenizing drought impacts throughout the heterogeneous landscape. This suggests that, in conservation and rangeland savannas where herbivores are key determinants of vegetation structure (Holdo et al., 2009; Sankaran, Augustine, & Ratnam, 2013; Staver & Bond, 2014; Staver, Bond, Stock, Rensburg, & Waldram, 2009), our current focus on the local, physiological effects of drought is probably insufficient. Landscape processes, including animal movement, are probably also critical (see also Ngugi & Conant, 2008; Butt et al., 2009; Anderson et al., 2010), such that evaluations of drought impact should expand to include this larger scale of analysis. That experimentation may not be possible at this larger scale should not prevent more comprehensive observational analysis. Predicting the effects of increasingly frequent droughts on savanna ecosystems will depend on it.

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## AUTHORS' CONTRIBUTIONS

A.C.S. analysed data and wrote the manuscript, with substantial feedback and discussion from all authors. C.W.-C. and J.B. coordinated data collection and curation.

## DATA ACCESSIBILITY

Data are available on South African National Park Data Repository <http://dataknp.sanparks.org/sanparks/metacat/judithk.111839.1/sanparks> (Staver, Botha, & Wigley-Coetzee, 2018).

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## SUPPORTING INFORMATION

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