

# Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns

Jason E. Donaldson<sup>1</sup>  | Sally Archibald<sup>1</sup> | Navashni Govender<sup>2</sup> | Drew Pollard<sup>1</sup> | Zoë Luhdo<sup>1</sup> | Catherine L. Parr<sup>1,3</sup>

<sup>1</sup>School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg-Braamfontein, South Africa

<sup>2</sup>Scientific Services, Kruger National Park, Skukuza, South Africa

<sup>3</sup>School of Environmental Sciences, University of Liverpool, Liverpool, UK

## Correspondence

Jason E. Donaldson  
Email: jedonaldson6@gmail.com

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## Abstract

1. Variation in grass height is beneficial to biodiversity conservation in savanna landscapes. Theory predicts that small fires can promote short-grass areas within savannas. We experimentally assessed the influence of fire season and size on grass height and the resultant response of wild grazer communities and tested three hypotheses: (1) repeated small fires in tall-grass savannas increase short-grass grazer densities in the post-burn environment; (2) increased grazer densities maintain grass height in a short, palatable state and drive feedbacks that exclude fire; and (3) late-dry season burns concentrate grazers more effectively than early dry season burns.
2. We repeatedly applied annual treatments (unburned, early- and late-burns) in 0.25-, 5- and 25-ha plots over a period of 3 years in a tall-grass savanna system in Kruger National Park, South Africa. Dung counts for grazer density and grass height data were collected along 50-m transects. Grass height was measured in paired 1-m<sup>2</sup> herbivore exclosures on plots before and after applied fires.
3. Dung data indicate that wildebeest occurred most frequently in grass heights below 5 cm. Their preference for plots regardless of fire size or season increased over time with each repeated burn. Zebra and buffalo favoured burns immediately post-fire, but buffalo did not actively select for burnt areas over longer time periods.
4. By the second year of treatment, herbivory maintained 28% and 91% of the grass height below 10 cm in the early- and late-season burns respectively. In contrast, herbivory on the unburned treatments had no effect on grass height.
5. *Synthesis and applications.* Fires less than 25 ha in size attracted sufficient grazing herbivores to shorten grass height. Repetition of the fire treatments resulted in the active selection of these areas in the longer term by wildebeest, impala and, to a lesser degree, zebra. Grazing pressure was high enough to initiate positive feedbacks and maintain lawns after only two seasons of burning and, depending on the season of burn, reduced grass height to a level that excluded repeat fires. Our study demonstrated that theory on grazer use of the post-fire environment can be implemented practically by applying small repeated burns to promote the formation of short-grass areas within savannas.

## KEY WORDS

African savannas, burn area, burning, fire ecology, grass system-state, grazer ecology, grazing, grazing lawns, herbivore

## 1 | INTRODUCTION

Grazers and fire act as competing consumers within savannas, with fires being most prevalent in tall-grass vegetation characterized by low herbivory, and grazers being most abundant in short, heavily grazed grasslands without enough fuel to burn (Archibald & Hempson, 2016; Staver, Bond, Stock, van Rensberg, & Waldram, 2009). Both grasses and woody plants show evidence for specialization to either frequently burnt (Ripley et al., 2015) or heavily grazed (Díaz et al., 2004) communities, leading to the realization that alternative system states, representing either a “brown” or “black” world (heavily grazed vs. frequently burnt) can occur in savanna landscapes (Bond, Woodward, & Midgley, 2005). Despite this, fire and herbivory are not mutually exclusive and often act together in savannas with effects on primary production, plant-soil nutrient pools and the species composition of vegetation (Knapp, Briggs, Blair, & Turner, 1998; van de Vijver, Poot, & Prins, 1999). Moreover, interactions between fire and grazers in savanna systems have resulted in a long history of fire manipulation by land users for the management of both livestock and wild herbivore populations (Collins & Wallace, 1990; Fowler & Konopik, 2007; Trollope, 1989).

The importance of fire in maintaining grass quality and quantity in rangeland systems is well recognized (Collins & Wallace, 1990). Globally, livestock farmers use fire to improve forage quality by removing moribund, low-nutrient grass biomass. This practice has resulted in a substantial body of literature focusing on managing fires for specific grassland conditions (biomass, height and graze quality) to maximize cattle production (Cibils, Borrelli, & Humano, 1998; Fensham, Holman, & Cox, 1999; Jones, 2000; Tainton, 1999). Until recently, similar studies on wild herbivore populations have been limited (but see Fuhlendorf, Engle, Kerby, & Hamilton, 2009; Klop & van Goethem, 2008; Sensenig, Demment, & Laca, 2010); consequently, fire management of wild areas has largely been informed by agricultural research. However, managers in some protected areas in Africa recognized that reliance on agricultural studies was inappropriate in savannas where grazer diversity is high and rejected the implementation of agricultural-based fire management (Biggs & Potgieter, 1999; van Wilgen, Govender, Biggs, Ntsala, & Funda, 2004). Recent work from east and west African savannas has justified their caution, demonstrating that fire size and frequency drives resource partitioning in communities of wild herbivores due to differences in energy requirements related to body size, digestive capabilities and the related stem to leaf, and Nitrogen to Carbon, ratios (Klop & van Goethem, 2008; Sensenig et al., 2010). In addition, wild ungulate populations vary in their utilization of different grass communities seasonally, with burnt areas, short unburned grazing lawns and tall-grass systems representing valuable resources at different times of the year (Augustine & Derner, 2014; Yoganand & Owen-Smith, 2014). Furthermore, in systems with predators, the increased visibility provided by short-grass patches can reduce predation risk, consequently attracting a range of prey species. Clearly to conserve a diverse suite of herbivores, it is desirable to have a diversity of grass sward heights in the landscape.

The majority of grazing species in savanna landscapes benefits from and responds to the highly nutritious regrowth after fire that replaces low-nutrient moribund grass. However, fires generally occur over large areas and can have homogenizing effects on the landscape, with the post-burn flush dispersing herbivores more evenly and allowing grass to “escape” grazing pressure uniformly (Archibald, Bond, & Fairbanks, 2005; Hobbs, Schimel, Owensby, & Ojima, 1991). This results in feedbacks that promote tall, unpalatable, fire-adapted grass communities (Archibald & Bond, 2004; Archibald et al., 2005), which may support some bulk-feeding herbivores (Estes, Atwood, & Estes, 2006; Trollope, 1995), but which reduce the diversity of grazers and grazing habitats overall. In contrast, small-scale disturbances such as mowing and nutrient addition that concentrate grazing within tall-grass savannas have been shown to facilitate the formation of grazing lawn systems (Cromsigt & Olff, 2008). Thus, it is possible that frequent small-scale fires that concentrate grazers on high-quality post-burn graze could also attract and maintain high numbers of grazers and drive a shift in grass communities towards shorter lawn systems that exclude fire. Here, we use an experimental approach to test the influence of fire season, size and return time on grass height and the resultant response of wild grazer communities. In addition to burn size, we predict that burn season will influence herbivore response to the post-fire green flush. Since the high-quality graze environment of the late-dry season burns provides a valuable resource for grazers during a resource poor period of the year, we predict that late-season burns will have a greater “magnet” effect on grazers than early dry season fires (Augustine & Derner, 2014; Yoganand & Owen-Smith, 2014).

We defined grazing lawns as areas where high grazing pressure limits grass height below levels required to carry fire, that is, grazing lawns are formed when positive feedbacks promote their maintenance and restrict fire. Based on this definition, we developed three hypotheses related to the formation of grazing lawns by repeated small-scale burning: (1) small fires (similar in size to known grazing lawns formed by other grazer-concentrating disturbances) in tall-grass savannas will result in increased short-grass grazer densities in the post-burn environment, with relatively smaller burns demonstrating greater responses; (2) increased grazer densities will maintain grass height in a short, palatable state and drive feedbacks that exclude fire and promote a grazer driven system; and (3) late-dry season burns will concentrate grazers more effectively than early dry season burns and result in a quicker transition to a grazing lawn state.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

Kruger National Park (KNP, S 24°23'35.17", E 31°46'41.13") in South Africa contains the full suite of large African mammals and provides an exception to many African national parks with nearly a century of detailed records on fire history and policy changes (van Wilgen et al., 2004). This makes KNP ideal for studies on the effect of different fire regimes on wild ungulate populations. Management of fires in KNP is currently based on available fuel loads, with management initiating

burns when grass biomass is high; fire return times thus vary across the park with rainfall and soil patterns resulting in different grass productivity and biomass accumulation rates (Govender, Trollope, & van Wilgen, 2006). The high fuel loads associated with these burns have resulted in a shift towards larger, higher intensity fires. Variation in the burn regime is generated through changes in season of ignition and intervals between burns. Fire management is focused on increasing heterogeneity within KNP (Govender et al., 2006; van Wilgen et al., 2004). Because the current KNP burn regime results in large fires, short-grass grazing lawns that support high grazer densities and rely on positive feedbacks associated with frequent grazing should be limited in distribution as animals are drawn off by large, frequent fires in the broader landscape (Archibald et al., 2005). This appears to be the case, with grazing lawns restricted to areas of high white rhinoceros (*Ceratotherium simum*) densities or areas where small-scale disturbances such as termite mounds, mud wallows and dung middens have resulted in unusually high grazer usage (Cromsigt & te Beest, 2014).

The Satara Land System, one of four major land systems in KNP, is characterized by clayey basalt soils (Venter, Scholes, & Eckhardt, 2003), supporting extensive C<sub>4</sub> grass plains in a *Sclerocarya birrea*–*Acacia nigrescens* tree savanna (Gertenbach, 1983). This area is currently dominated by C<sub>4</sub> grasses *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, *Urochloa mosambicensis* and *Themeda triandra* (Knapp et al., 2012; van Oudtshoorn, 2012), with the high abundance of unpalatable *B. radicans* presenting a concern to land managers. The growing season for grasses occurs during the austral summer (November–April), during which 78% of the mean annual rainfall of 502 mm/year falls (Venter et al., 2003). Grasses are dormant during the dry, frost-free winters (May–October). Prior to this experiment, the area had an average fire return interval of c. 3 years.

A complete suite of indigenous herbivores occur in relatively large abundances within the Satara Land System (du Toit et al., 2003); however, for this study we focus on the four major grazer species (African buffalo [*Synacerus caffer*], impala [*Aepyceros melampus*], blue wildebeest [*Connochaetes taurinus*] and plains zebra [*Equus quagga*]) due to low dung counts for the remaining species. African elephant (*Loxodonta africana*) were excluded due to high levels of browse in their diets. Buffalo, impala and wildebeest are all ruminants with studies in KNP showing that 88%, 60% and 90% of their diets are made up of C<sub>4</sub> grasses respectively (Codron et al., 2007). Buffalo require large amounts of coarse biomass and tend to be found in grass heights above 20 cm, while wildebeest and impala require high-quality graze and feed more regularly in short-grass areas (<10 cm) (Kleynhans, Jolles, Bos, & Olff, 2010). Zebra digest their food using hind-gut fermentation and feed almost exclusively on C<sub>4</sub> grasses (Codron et al., 2007) and ubiquitously across grass heights (Kleynhans et al., 2010).

## 2.2 | Experimental design

To test the influence of fire season and size on grazers and the effect of post-burn herbivory on grass state, we implemented a landscape level experiment between January 2013 and January 2016. We selected three treatment plot sizes: 50 × 50 m (0.25 ha), 220 × 220 m

(5 ha), 500 × 500 m (25 ha). These sizes were chosen to represent the three most common short-grass areas in KNP: termite mounds (20–50 m<sup>2</sup>—see Davies et al., 2014), naturally occurring sodic site (c. 250 m<sup>2</sup>—see Grant & Scholes, 2006), and large grazing lawn systems (c. 500 m<sup>2</sup>–1 km<sup>2</sup>—see Yoganand & Owen-Smith, 2014). The 0.25- and 5-ha plots were replicated four times for each of the three treatments, with fire either completely excluded (unburned treatment) or with burns applied annually in the early dry season (April/May, hereafter referred to as early burns) or late-dry season (September/October, hereafter referred to as late-burns). However, due to space constraints and logistical issues, we were only able to implement three late-burn 25-ha plots. The experimental setup thus had three fire treatments (unburned, early- and late-burns), two fire sizes (0.25 and 5 ha) with four replicate plots and an additional three 25-ha late-burn plots, resulting in a total of 27 treatment plots.

Fires were applied every year by experienced teams from “Working on Fire” (<http://workingonfire.org>) to each of the early- and late-burn treatment plots, resulting in three burn applications per plot by 2016. Plots were selected that had: (1) high grass biomass with grass communities dominated by the fire climax grasses *B. radicans* and *T. triandra*, (2) similar amounts of woody cover and (3) similar abiotic conditions. Sampling effort needed to be higher on the larger plots required greater sampling effort to represent the variability in grass heights over the larger areas. We, therefore, created a 50 × 50 m subplot sampling design that could be implemented in the 0.25-ha plots and was replicated on the 5- and 25-ha plots four and nine times respectively. We erected 1-m<sup>2</sup> herbivore exclosures in the centre of each subplot to enable us to assess the effect of fire alone, and we sampled two parallel 50-m transects placed an equal distance on either side for analysis of combined fire–herbivore effects.

## 2.3 | Data collection

To estimate burn patchiness, we walked the two transect lines of each subplot immediately after burning and recorded burnt/unburned patches every 2 m. A burn patchiness index was calculated using equation:

$$1 - (\text{Burnt points/total points} - (\text{unburnt points/total points} \times \text{number of unconnected burn points/total points}))$$

This gave a value between 0 (all points burnt) and 1 (no points burnt) with weight for the contiguity of the burn (Table 1).

Data on grazer densities and grass biomass were collected using a BACI approach (before-after control-impact) (Smith, 2002). Sampling took place 1 month prior and for 2 months after application of seasonal-burns on both the fire-treated and unburned plots. We sampled early burn plots again in December 2013 when the first major rains of 2013/2014 arrived to account for herbivore responses to fresh growth on these plots. Due to logistics, this meant the second month of post-burn sampling for late-burn plots occurred in January 2014. Finally, we sampled all plots again at the end of the rainy season in April when grass biomass was expected to be highest. Thus, the first data collection occurred in April

**TABLE 1** Overview of plot characteristics for all fire application treatments in 2013. Reported grass heights were measured before the application of fire treatments

Treatment	Size (ha)	Number of plots	Mean distance to water (km)	Woody cover (%)	Mean grass height (cm)	Burn patchiness index
Unburned	0.25	4	1.5 (1.2)	6.8 (3.9)	37.2 (6.7)	NA
	5	4	1.6 (1.2)	7.6 (2.3)	43.2 (3.2)	
Early burn	0.25	4	1.4 (1.0)	7.6 (1.7)	56.4 (6.3)	0.28 (0.13)
	5	4	1.2 (1.3)	6.1 (3.9)	56.7 (6.3)	0.46 (0.02)
Late-burn	0.25	4	1.8 (1.6)	8.6 (3.8)	37.0 (0.9)	0.08 (0.17)
	5	4	2.7 (1.9)	6.3 (0.7)	40.1 (4.7)	0.01 (0.01)
	25	3	1.3 (1.1)	6.6 (1.6)	37.6 (3.9)	0.01 (0.01)

2013 with early burn and late-burn treatments applied in May and October 2013, respectively, and repeatedly every year thereafter until 2016.

Vegetative response to fire and grazing was recorded every 5 m along the two transect lines in each subplot. At each point, we measured the grass height of the standing grass biomass. We took the same measurements at five points within the herbivore exclosures to assess grass response in the absence of herbivory.

Grazer presence was measured by recording all dung (species and abundance) including dry dung encountered in 4-m-wide belts along transect lines. Dung transects have been used previously to estimate large herbivore habitat usage in long-term studies within African savannas and perform better than direct observations and other indirect measurements (Burkepile et al., 2013, 2016; Cromsigt, van Rensberg, Etienne, & Olff, 2009), giving relatively reliable measures for comparisons of relative abundance across similar habitats (Marques et al., 2001; Sensenig et al., 2010). Despite this, decomposition rates on different substrates and dung removal rates by dung beetles represent two inherent issues with using dung counts to assess large mammal abundance in savannas. These issues are not easy to mitigate with changes to methodology but were taken into account when drawing conclusions from our results. Fortunately, in the context of this study both factors would result in an under-representation of the expected response, not a false-positive: the increased bare ground on burnt plots would have increased dung decomposition and removal (Davis, Scholtz, Kryger, Descholdt, & Strümpher, 2010), resulting in under-representation of dung counts on burn treatment plots when compared with unburned plots. Finding increased dung on the burn plots is therefore evidence for substantial herbivore utilization. Furthermore, dung beetle activity is higher during the warm wet summers (November–April) than during cold dry winters (May–October) (Davis, 1996) and would have removed more dung during summer post-burn sampling than winter sampling. To eliminate any further bias and ensure that the time period of sampling was equal, we walked and cleared transects of dung 1 month prior to initial data collection. Dung counts were then sampled on a precise monthly (30 day) basis with dung crushed during data collection to avoid recounting. Dung counts per transect were divided by days since previous sampling (30) and the mean dung deposition per week was calculated per species for each plot.

Monthly rainfall data were recorded from the Satara Rest Camp and Singita Lebombo staff village weather stations (Figure 1).

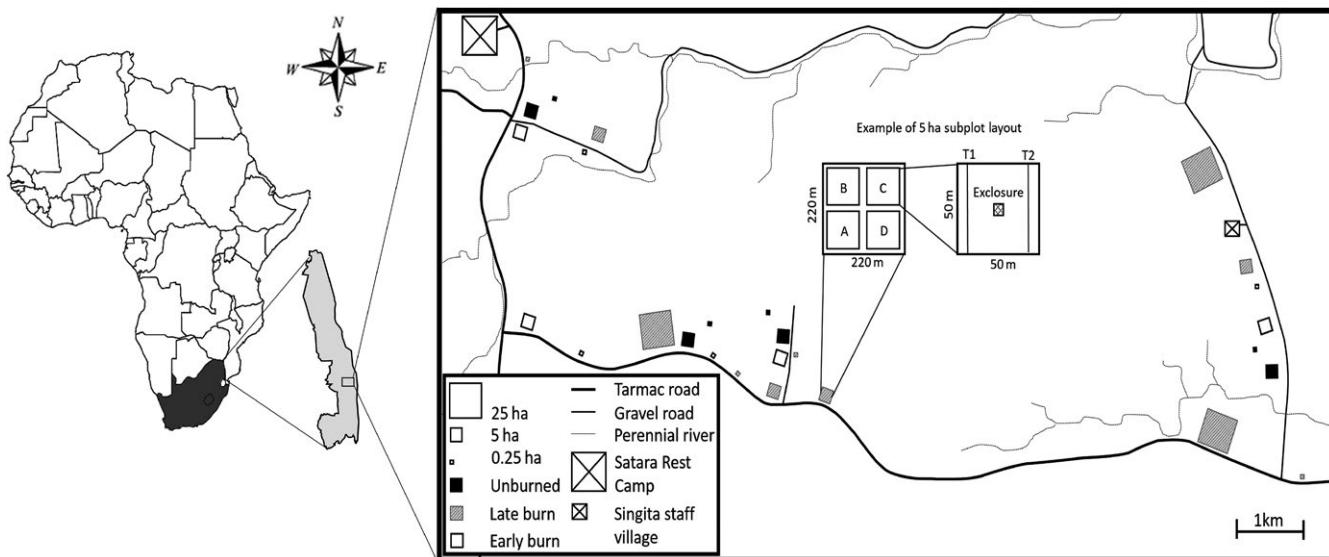
## 2.4 | Data analysis

We modelled grazer dung events per week (as a proxy for abundance) using a generalized linear mixed effect model (GLMM) with a Poisson distribution to assess the response of all grazers to early- and late-burns of different sizes (Crawlet, 2013). Burn size (0.25, 5 and 25 ha for late-burn), distance to water and month represented fixed effects with plot and subplot acting as nested random effects to control for repeated measures along the transects of each subplot every month.

Following Sensenig et al. (2010), we calculated a grazer preference index for species in each treatment plot as the total of dung in a burn treatment plot divided by the sum total of dung in the burned treatment and matched unburned treatment plot. In the case of 5-ha plots, this meant summing the dung across all transects in all subplots prior to calculating the ratio. This gives a value of 0–1 for each early- or late-burn plot, with 0 (total avoidance) and 1 (complete preference for burn treatments). Late-burn 25-ha treatments did not have matched unburned plots and were excluded. We modelled the preference of the four focal grazing species to burn treatments over the 3 years of the experiment using GLMMs with a binomial distribution. For each species, the grazer preference index for each plot represented the response variable with fire size (0.25 and 5 ha), distance to water, and treatment (early burn and late-burn) acting as fixed effects. Plot represented the random effect to control for repeated sampling of plots every year.

To assess what grass height each species of grazer selected throughout the final year of treatment (2015), we binned transect lines by their mean grass height in 5-cm increments from 0 to 40 cm. For each grazer species, we recorded a presence if any dung event occurred along the transect line and an absence if no dung was found. These scores were tallied to give the proportion of presence for a given number of transect lines of a specific grass height class. We ran a Chi-square test to compare observed grazer frequency within the different grass heights to the distribution of sampling effort (Crawlet, 2013).

We ran two statistical models on our grass height data. To assess whether our treatments kept grass short throughout the growing



**FIGURE 1** Layout of burn treatments in the Satara Land System of Kruger National Park. Late-burn and early burn plots were burnt in May and October of every year of the study while no fire occurred in the unburned plots or on the remaining landscape. The 5- and 25-ha plots contained four and nine  $50 \times 50$  m sampling subplots, respectively, while 0.25-ha plots were the equivalent of a single subplot. We erected herbivore exclosures ( $1 \text{ m}^2$ ) in the centre of each subplot to enable us to assess the effect of fire alone, and we sampled two parallel 50-m transects (T1 and T2) placed an equal distance on each side for analysis of combined fire–herbivore effects. All data collection took place along the transect lines and within exclosures of every subplot. Sampling of all subplots occurred every year before and after burn treatments

season, we assessed grass height in April (end of the growing season) over the 3-year study period using linear mixed models (LMM) with the restricted maximum likelihood method. Burn size (0.25, 5 and 25 ha for late-burn), grazing (presence/absence) and year (2013, 2014, and 2015) represented fixed effects, with plot and subplot acting as nested random effects. For this analysis, we modelled each fire treatment (unburned, early burn and late-burn) separately to enable interpretation of results. We compared the cumulative effect of our fire/grazing treatments on grass height over the 3 year experiment (with April 2015 grass height as the response variable). The fixed effects included treatment (unburned, early burn and late-burn), size (0.25 and 5 ha) and grazing (presence/absence), while plot and subplot were included as nested random effects.

All LMMs and GLMMs were processed using R statistical software (version 3.3.1; R Development Core Team, 2009) and the lme4 package (Bates, Machler, Bolker, & Walker, 2015). Following the suggestions of Zuur, Ieno, and Smith (2007) and Bolker et al. (2009), we used a top-down approach to model selection with an ANOVA to remove effects that resulted in models that did not differ ( $p < .05$ ) significantly from the full model (Table 2). We looked for obvious deviations from homoscedasticity and overdispersion in our models by plotting residuals against fitted values and visually assessing plots. To verify normality of the residuals of selected models, we used the Shapiro–Wilks test and assessed histograms and QQ plots visually (Zuur et al., 2007). We ensured that sampling subplots were not spatially auto-correlated by utilizing the georR package (Ribeiro & Diggle, 2016) to calculate semi-variograms for raw data for each year of sampling and using the residuals from all selected models (Zuur et al., 2007). Semi-variograms showed that variation in direct measures of grass height and dung counts, as well as residuals, did not increase with increasing distance

between plots, indicating no serious autocorrelation issues were present (see Figure S1 and Table S1). Since the GLMM for buffalo burn preference indices showed that residuals were not normally distributed with clear overdispersion, we used a negative-binomial distribution to improve model performance (Zuur et al., 2007).

## 3 | RESULTS

### 3.1 | Grazer burnt area and grass height preference

Grazers clearly responded to fire treatments with dung events increasing in abundance on burn plots after fire treatments were applied in 2013 (Figure 2). The GLMM confirmed that for both early burn ( $ES = 1.89, SE = 0.56$ ) and late-burn ( $ES = 4.22, SE = 0.24$ ) plots, the months after the fire were strong predictors of grazer densities. For the early burn, grazer densities increased immediately after the fire and further increased in December after the first major rains of the 2013–2014 season (Figure 2). Similarly, the late-burn treatment GLMM demonstrated that grazers responded strongly to burn treatment in the months after fire application, with the strongest response in the first month post-fire ( $ES = 2.63, SE = 0.11$ ).

Densities remained high until January 2014. We found no evidence to suggest that fire size affected these relationships for either early ( $ES = 0.14, SE = 0.10$ ) or late-burn ( $ES = -0.02, SE = 0.01$ ) treatments, perhaps due to low sample size for dung transects per month.

Wildebeest showed no preference for burn plots prior to treatment in 2013, but switched to actively selecting and staying on both early- and late-burn treatments in the following 2 years (Figure 3—GLMM  $ES = 0.26, SE = 0.09$ ; Figures S3 and S4). Impala had a constant preference for burnt treatments through over the study period ( $ES = -0.05,$

**TABLE 2** Linear mixed models and generalized linear mixed models used to assess the relationships between herbivore selectivity of plots and the effects of different grazing and fire regimes on grass height. In cases where no fixed effects showed any relationship with the response variable, null models were selected and more complex models are only shown to indicate effects tested

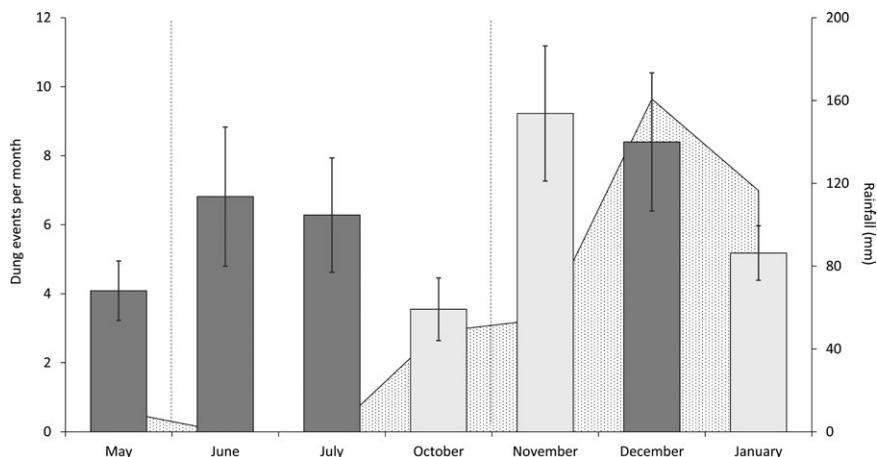
Selected models	df	F	p
Wildebeest			
Burn preference index ~ Year + (1 plot)	2	13.1	.001
Impala			
Burn preference index ~ Year + (1 plot)	2	0.9	.607
Zebra			
Burn preference index ~ Year + (1 plot)	2	3.5	.17
Buffalo			
Burn preference index ~ Year + (1 plot)	2	0.3	.843
Unburned			
Grass height ~ Year + (1 plot subplot)	2	123.4	<.0001
Early burn			
Dung density ~ Month + (1 plot subplot)	4	156.4	<.0001
Grass height ~ Year * Grazing + (1 plot subplot)	3	7.8	.05
Late-burn			
Dung density ~ Month + (1 plot subplot)	4	156.9	<.0001
Grass height ~ Year * Size * Grazing + (1 plot subplot)	12	318.9	<.0001
All 5-ha treatments in year 2015			
Grass height ~ Grazing + (1 plot subplot)	2	24.5	<.0001

$SE = 0.06$ ) but increased in plot utilization year on year (Figures S3 and S4). In contrast, zebra ( $ES = 0.06$ ,  $SE = 0.08$ ) and buffalo ( $ES = -0.11$ ,  $SE = 0.16$ ) showed no significant changes in their preference indices over the study period (Figure 3) and other than an initial response to early burn treatments showed no long-term increases in densities over the study period (Figures S3 and S4). The burn preference ratios showed no effect of fire size ( $ES = 0.02$ ,  $SE = 0.02$ ) or fire season ( $ES = -0.03$ ,  $SE = 0.09$ ). Wildebeest ( $\chi^2 = 139.9$ ,  $p < .001$ ) and impala ( $\chi^2 = 38.84$ ,  $p < .001$ ) were also found unexpectedly often in grass heights below 10 cm across the study sites in 2015 and were found rarely in grasses above 25 cm. Zebra occurred uniformly across all grazing height classes between 0 and 40 cm. Buffalo occurred more frequently in grass heights above 15 cm ( $\chi^2 = 35.76$ ,  $p < .05$ ) than

expected and were seldom found in short-grass areas below 5 cm. Thus, although all grazers clearly responded to the fire treatments in the short-term, only wildebeest appear to have been driving the longer term grass height differences between plots.

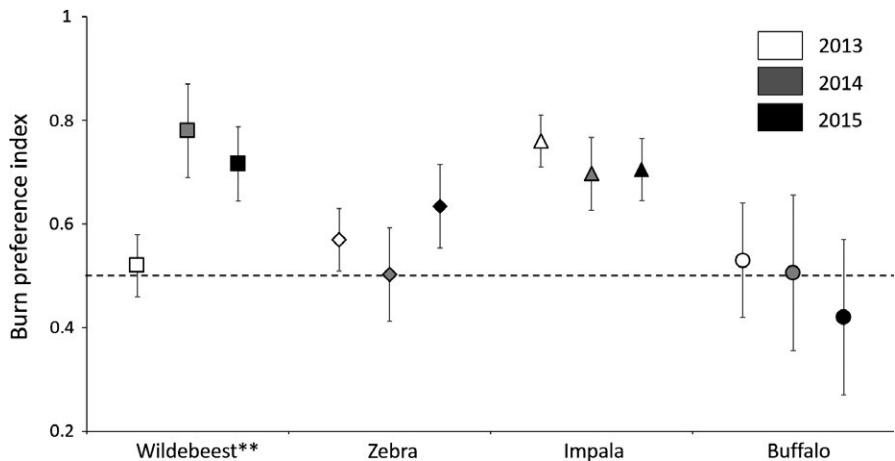
### 3.2 | Grass system response to fire and herbivory

Grass height at the end of the season decreased on all plots over the course of the study (Figure 4) due to lower rainfall and moribund grass on unburned plots in the 2014–2015 season ( $ES = -13.6$ ,  $SE = 0.59$ ). We did not find any evidence that grass height on unburned plots was affected by grazing ( $ES = -3.60$ ,  $SE = 0.89$ ) or size ( $ES = 2.00$ ,  $SE = 0.78$ ). Likewise, the grass on burn-only treatments

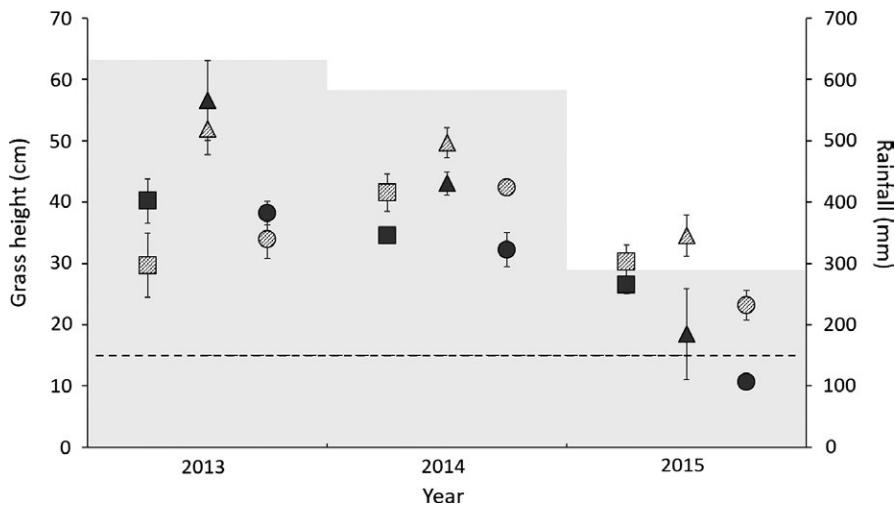


**FIGURE 2** Dung deposition per month ( $M \pm SE$ ) and rainfall (hatched) for each month of 2013 when the early- and late-burn fire treatments were initiated. Data was sampled on early burn (dark grey) and late-burn (light grey) plots for 1 month prior- and 2 months' post-fire application. Dashed lines represent fire application in May and October 2013 for the eight early burn and 11 late-burn plots respectively

**FIGURE 3** Burn preference indexes (0 = absolute avoidance of burnt plots, 1 = complete preference for burnt plots) for 3 years of fire treatments for grazing herbivores in the Kruger National Park. Data for 2013 is prior to any burn applications with 2014 and 2015 representing the responses of grazers to one and two seasons of burning respectively (\*\* $p < .001$ )



**FIGURE 4** Grass height ( $M \pm SE$ ) and total annual rainfall (light grey) on unburned (squares), early burn (triangles) and late-burn (circles) plots for 3 years of fire treatment implementation. Grass height decreased in 2015 due to rainfall regardless of treatment. Fire treatment alone (light grey and hatched) had no effect on grass height, but the coupling of herbivory and fire treatment (dark grey) decreased grass height on early burn and late-burn plots after 2 years of treatment. The dashed line represents the upper limit of grass height (15 cm) that wildebeest actively select



(exclosures) regrew to pre-fire levels by the end of the season (early burn  $ES = -3.50$ ,  $SE = 1.41$ ; late-burn  $ES = 7.85$ ,  $SE = 2.95$ ), while grass height decreased dramatically as a result of lower rainfall and fire treatments by 2015 in early- ( $ES = -21.56$ ,  $SE = 8.37$ ) but not late-burn plots ( $ES = -1.45$ ,  $SE = 3.00$ ) resulting in the exclosures grass (all treatments) being c. 30 cm by 2015. The attractive effect of fires on grazers, however, resulted in an even greater decrease in grass height by 2015 for both early burn ( $ES = -28.73$ ,  $SE = 8.44$ ) and late-burn ( $ES = -22.36$ ,  $SE = 3.06$ ) treatments (Figure 4). Consequently, after 3 years, the burned-grazed plots were the only ones with grass  $<20$  cm on average, with large proportions of the grass  $<5$  cm on late-burn plots (Table 3). Repeated attempts to ignite plots in 2015 failed in half of the early burn and all late-burn treatments (Table 3).

There was no evidence that the size of fire affected grass height for early burn treatments ( $ES = -1.55$ ,  $SE = 1.30$ ). However, the LMM for late-burn treatments indicated that there was some effect of fire size on the time it took for grazers to maintain grass in a cropped state. Herbivory on the smallest burns (0.25 ha) resulted in the maintenance of a relatively short-grass state ( $<25$  cm) after the first season of treatment ( $ES = -15.28$ ,  $SE = 9.22$ ), while a similar response was only seen in the second year of treatment for the two larger burns (5 ha  $ES = -14.60$ ,  $SE = 11.13$ ; 25 ha  $ES = -16.84$ ,  $SE = 10.67$ ). Grass height

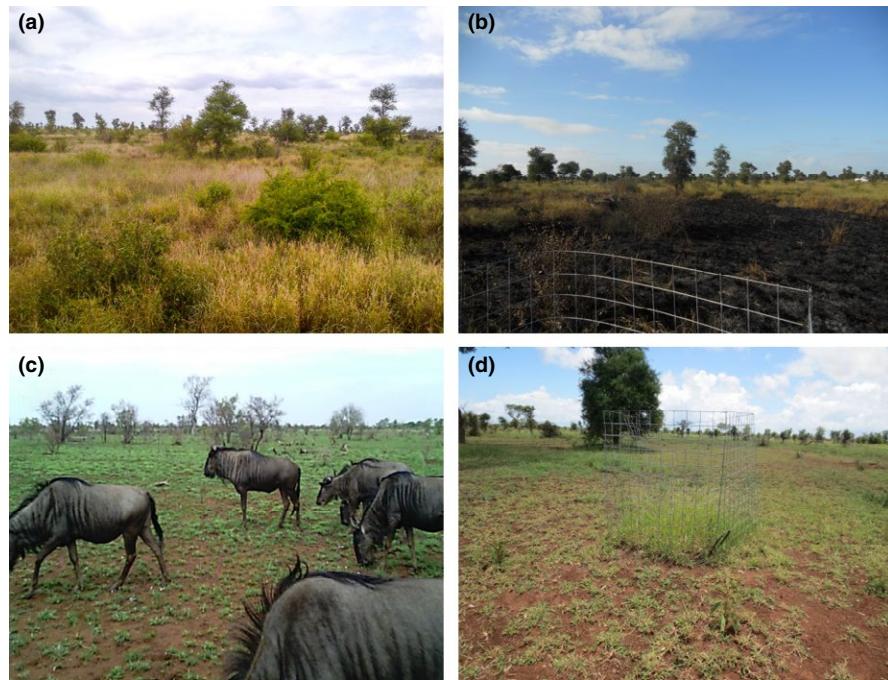
was also kept  $<5$  cm on average by herbivores on the smallest fires, while grass height was maintained  $<15$  cm on both 5- and 25-ha plots by the final year of the study.

#### 4 | DISCUSSION

Our study demonstrates that it is possible to engineer landscapes by applying ecological theory to achieve particular goals. Small fires ( $<25$  ha) attracted all the grazing herbivores studied in large enough numbers to initially shorten grass height, particularly during the wet season. This immediate herbivore response after the first burns was not sufficient to maintain grass communities in a short lawn state over the growing season. However, repeated applications of fire treatments over the following 2 years resulted in short-grass specialists (wildebeest) actively selecting for burnt patches over the entire growing season. Ultimately, the high densities of impala, wildebeest and to a lesser extent zebra on burnt plots (see Figures S3 and S4) maintained lawns after the second season of burning and, depending on the season of burn, reduced grass height to a level that excluded repeat fires (Figure 5). Theory predicts that at least 40% of a landscape needs to be non-flammable ( $<c. 5$  cm) to restrict fire spread (O'Neill, Gardner,

**TABLE 3** Overview of plot characteristics for all fire application treatments in 2015

Treatment	Number of plots	Mean proportion of grass height below 10 cm	Mean proportion of grass height below 5 cm	Number of plots where repeat ignition failed	Bare ground (%)
Unburned	8	0.08 (0.04)	0.06 (0.02)	NA	11.4 (1.2)
Early burn	8	0.28 (0.04)	0.11 (0.03)	2	34.1 (1.3)
Late-burn	11	0.91 (0.03)	0.80 (0.04)	11	36.6 (1.5)



**FIGURE 5** Sequence of photos depicting changes in vegetation in response to experimental treatments in the 5-ha late-burn plots in Kruger National Park. From top left: (a) grass structure pre-burn (April 2013); (b) burnt area immediately post-burn (October 2013); (c) wildebeest grazing response to post-burn green flush (November 2014); (d) differences in grass height within and outside of an exclosure after two seasons of burn treatments (April 2015)

Turner, & Romme, 1992). This was achieved on all our late-burn plots by the end of 3 years, but only 25% of the early burn plots—with the expected response of switching off fire being evident during our 2015 burns (Table 3). Moreover, grass height <10 cm is preferred by wildebeest and >90% of the late-burn and 25% of early burn grass cover was in this state by the end of 2015 (Table 3).

Four of the 32 extant large grazing mammals in Africa are short-grass specialists (see Table S1)—these species (like wildebeest) often make up a large proportion of herbivore biomass across their range (Hempson, Archibald, & Bond, 2015). Moreover, the greater visibility on short-grass areas means that many other large herbivores gain additional benefits, including improved predator detection and avoidance and show a preference for utilizing short-grass areas (Anderson et al., 2010; Burkepile et al., 2013; Kleynhans et al., 2010). Short-grass specialists are common in lower rainfall savannas, which make up 50% of sub-Saharan Africa (Hempson et al., 2015); in these areas, including the globally recognized Masai Mara, Serengeti, Etosha, Gorongoza, Chobe and KNPs, management to promote and maintain short-grass habitat should be integral to conservation management and wildlife breeders. Our results suggest that small fires used with specific management outcomes have the potential to engineer savanna grass communities into a short-grass state and diversify grass structure in a similar way to that of white rhinos and termitaria (Cromsigt & Olff, 2008; Cromsigt & Te Beest, 2014; Waldram, Bond, & Stock, 2008).

Initiation and maintenance of short-grass areas will be easier in drier regions (Waldram et al., 2008), but the use of repeated burning in the absence of other lawn drivers could be important in wetter regions and may represent a valuable tool where mega-herbivores are low in density or locally extinct in areas both within Africa and globally (Fuhlendorf et al., 2009).

#### 4.1 | Grazer burnt area and grass height preference

The active selection of our smallest burn treatments by all herbivores post-burn and by wildebeest over the period of the study supports our first hypothesis. This is a good indication of the importance of short-grass systems as resources for grazers during the breeding season and likely represents a lack of these areas in the general landscape. Furthermore, the long-term use and active selection for burnt plots by wildebeest, as well as the greater presence of both wildebeest and impala in short-grass areas, in contrast to buffalo, supports recent work by Burkepile et al. (2016) showing herbivore suite responses on long-term burn plots. Our findings align with work suggesting that grass height heterogeneity is an important factor in large-grazer resource partitioning in savannas (Burkepile et al., 2016; Cromsigt & Olff, 2008; Sensenig et al., 2010). Although analysing demographics is beyond the scope of this study, the strong selection bias of wildebeest for short-grass areas, and avoidance of tall-grass areas, seems pertinent

considering their below expected abundance in KNP (Yoganand & Owen-Smith, 2014) and highlights issues with using agricultural-style burning in natural ecosystems.

#### 4.2 | Grass system response to fire and herbivory

After only two seasons of burning, the fire-grazer effect initiated a new grass structural type in a previously tall-grass system and strongly supported our second hypothesis. Lower rainfall in 2015 and resultant reduction in grass productivity played a role in facilitating the switch to a short-grass state. However, the strong influence of herbivory, coupled with fire, on grass height leaves us confidence that this state would have been reached in subsequent seasons if rainfall had continued at levels seen in 2013 and 2014.

The more complete switch to short-grass state on late-burn plots when compared to early burns does not seem to be the result of higher grazing densities, as there was no difference in the response of herbivores to either treatment. This observation disputes our third hypothesis. It is possible that dung transect data were not detailed enough to provide a complete picture of the differences in herbivore use. Herbivores present but not feeding (i.e. resting or being vigilant) on plots and variation in dung deposition rates at different times of the year may have created too much noise in the data to allow us to identify subtle variations in plot usage. This makes it difficult to decipher the cause of the greater response of grass height to grazing on late-burn plots compared with early burn plots. While our data limit definitive conclusions, we know that the higher fuel moisture during the early burn season resulted in tall-grass clumps within early burns (note the large standard error of early burn means in Figure 3). These unburned clumps would have been avoided by herbivores and remained uneaten, and may also have acted to discourage consistent feeding due to increased predation risk and increased vigilance (Fortin, Boyce, Merrill, & Fryxell, 2004) potentially reducing effects on the grass layer (Fortin et al., 2004). Thus, while dung deposition is similar on early- vs. late-burn plots, direct grazing effects would be greater on late-burns.

The greater effect of grazing on smaller plots could again be the result of lower use by grazers spending a similar amount of time on plots. Wildebeest rest in sites where predator avoidance can be maximized (Owen-Smith, 2008), which would be greater on larger burn patches. Thus, similar dung densities on larger plots may reflect lower grazing intensity and explain the difference in grass heights.

#### 4.3 | Implications for ecosystem properties and management

The switch of the treatment plots to a short-grass state with greater bare ground (Table 3) increased structural and functional diversity of the landscape. Concentrated grazing and soil compaction by herbivores can shift grass community composition towards species more tolerant of water stress and heavy grazing (Cromsigt & Olff, 2008; Veldhuis et al., 2014). These potential changes will likely have cascading effects on other communities (Krook, Bond, & Hockey, 2007).

Grazing lawn systems have been shown to support suites of grasshoppers (Samways & Kreuzinger, 2001), birds (Krook et al., 2007) and spiders (Warui, Villet, Young, & Jacque, 2005) unique from tall-grass systems. In addition, ants respond rapidly to changes in bare ground (Parr, Robertson, Biggs, & Chown, 2004) and may have already responded to the structural changes experienced on the plots. However, it is also possible that there are negative effects of the treatments. Increased bare ground in plots may result in increased run-off and loss of top soil (Thornes, Wainwright, & Parsons, 1985), and subsequent switches to poor quality grass species (Cibils et al., 1998; Fensham et al., 1999). This is of concern on poor quality soils and in low rainfall areas. However, the response shown by short-grass specialists to small fires in this study was still apparent (Burkepile et al., 2016) in a nearby long-term burning experiment with similar fire treatments (7-ha blocks burned at various frequencies/seasons since 1955), indicating that this grass structural type can persist in the landscape and continue to create favourable habitat even 60+ years since initial treatments.

The practicality of implementing small burns over large areas in a national park also needs to be addressed. It appears that there is some flexibility in the size of fire needed to achieve the grazing lawn state: all our size treatments were equally effective at attracting grazing herds (i.e. none of our fires were large enough to result in the dispersal of grazers, nor small enough to not be noticed within the broader landscape). However, application of our experiment was labour intensive and required skilled teams to operate over several days, and keeping all other fires out of the surrounding landscape is not feasible. The danger of fires spreading during the late-dry season means that it would be difficult, in practise, for managers to carry out the same small fire application repeatedly over large areas. However, early season burns tend to be smaller, and frequently burn out naturally if not actively re-ignited. Use of small early season burns also align with current shifts in KNP fire management towards the use of earlier season fires in response to the increase in the number of large hot wildfires during the late-dry season that negatively affect tall trees in the park. Despite the more limited change on early season treatments, we believe this is the most realistic option to implement over broader areas in savannas across Africa. A greater number of repeated treatments is also likely to achieve the same result as late-burns given a longer period, especially if the occasional runaway fire results in temporary dispersal of grazing.

Variation in grass community structure and diversity of grass height is now widely accepted as necessary in the conservation of savanna landscapes (Owen-Smith, 2004). With the white rhinoceros, the main driver of large-scale short lawn creation, under threat in most natural systems, it is likely to become increasingly necessary for conservation managers to look at novel ways of manipulating the grass layer over wide areas. Here, we have experimentally shown that small-scale fires have the capacity to concentrate grazers in sufficient densities to maintain grass in a short-grass lawn state. Our findings indicate that theory on spatial patterns of grazer use of the post-fire environment developed by Archibald et al. (2005) can be practically implemented to promote short-grass areas within the landscape.

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## AUTHORS' CONTRIBUTIONS

S.A., K.P. and N.G. conceived the ideas with all authors designing the methodology; D.P., Z.L. and J.D. collected the data; J.D., S.A. and K.P. analysed the data; J.E.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the South African National Parks Data Repository. judithk.111311.2. <http://datakn.parks.org/sanparks/metacat/judithk.111311.2/sanparks> (Donaldson et al., 2017).

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