

RESEARCH ARTICLE

Small-scale fires interact with herbivore feedbacks to create persistent grazing lawn environments

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Abstract

1. Fire-herbivory feedbacks strongly influence the formation of grazing lawns in savanna ecosystems. Preliminary findings suggest that small-scale (<25 ha) fires can engineer grazing lawns by concentrating herbivores on the post-burn green flush; however, the persistence of such grazing lawns over the longer term and without repeated fire is unknown.
2. We used high-resolution Light Detection and Ranging (LiDAR) to investigate the long-term effects of fire manipulation on short grass structure (height, cover, volume and spatial continuity) and grazing lawn establishment in Kruger National Park, South Africa. We analysed the effects of fire exclusion and experimental burns applied over a 7-year period (2013–2019) followed by a 1-year cessation of burning at varying spatial scales during the early and late dry seasons.
3. Fires contributed a fourfold increase in short grass cover, regardless of fire season or size. The distribution of grass height differed significantly between fire-induced grazing lawns and recently unburnt parts of the landscape where controlled fires were excluded over the experimental period. The volume (corresponding to bulk density) of short grass on the landscape responded strongly to fires, with grass volume <20 cm in height increasing with both early and late dry season fires.
4. Early dry season fires caused larger and more homogeneous short grass patches. Furthermore, early dry season fires were more influential in increasing the cover of the shortest grass height class (1–5 cm).
5. *Synthesis and applications.* Our results demonstrate that fire-induced grazing lawns can persist over the longer term, even when fires are no longer applied, leading to the creation of vertical and horizontal heterogeneity in the grass layer. Small-scale fires, therefore, represent a feasible management approach to expanding grazing lawn extent, potentially benefiting grazer coexistence and diversity.

KEYWORDS

bulk density, fire manipulation, Kruger National Park, Satara, short grass cover, UAV-LiDAR

1 | INTRODUCTION

Grazing lawns are important features of savanna ecosystems, playing a key role in landscape heterogeneity through the creation of vegetation patchiness (Hempson et al., 2015). This patchiness promotes biodiversity while the high quality of grasses on lawns supports large herbivore populations (Cromsigt et al., 2017; Krook et al., 2007). Grazing lawns are characterized by communities of short-statured grasses with a high leaf to stem ratio and increased bulk density, which are predominantly maintained by the frequent concentration of high grazing activity (Cromsigt & Olff, 2008; Hempson et al., 2015). Frequent grazing keeps the grass short and concentrates nutrients through urine and dung deposition by herbivores, which in turn increases the digestibility of lawn grasses and encourages future foraging, thereby facilitating lawn persistence and preventing re-colonization by tall or bunch grasses (Coetsee et al., 2011; Verweij et al., 2006). The short grass on lawns also increases visibility, lowering predation risk and further attracting grazers to these highly productive areas (Gaynor et al., 2019; le Roux et al., 2018). In addition, the high productivity and forage quality within grazing lawns constitute preferred foraging sites for herbivores during the wet and early dry seasons (Verweij et al., 2006; Yoganand & Owen-Smith, 2014), which in turn, diversifies grazer populations (Hempson et al., 2015; Owen-Smith, 2004; Person et al., 2003).

Grazing lawns in savanna ecosystems can span several square meters to hectares in extent (Archibald, 2008) and exhibit variable levels of persistence that can span from a few months (Cromsigt & Olff, 2008; Davies et al., 2016) to decades (Novellie & Gaylard, 2013), with lawn persistence dependent on a sufficient abundance of megagrazers, such as white rhinoceros (*Ceratotherium simum*) and common hippopotamus (*Hippopotamus amphibius*), on the landscape (Cromsigt & te Beest, 2014; Voysey et al., 2023; Waldram et al., 2008). In locations with low or decreasing megaherbivore abundance, expanding grazing lawns beyond hotspots of nutrient enrichment, such as riparian areas (Kanga et al., 2013), termite mounds (Davies et al., 2016), sodic sites (Grant & Scholes, 2006; Verweij et al., 2006) or abandoned cattle corrals (Porensky & Veblen, 2015), remains a challenge.

Fires are an important modifier of grassland structure and function (Archibald et al., 2005; Gordijn & O'Connor, 2021) and have been shown to influence spatio-temporal patterns of grazing (Archibald & Bond, 2004; Burkepile et al., 2016; Parrini & Owen-Smith, 2010). However, the role of fire in influencing grazing lawn establishment and persistence is less well understood. Fires improve forage quality in the short term by removing unpalatable, moribund herbaceous biomass and stimulating growth with higher bulk density and nutritional quality (Anderson et al., 2007). Such post-fire grass regrowth creates a 'magnet effect' on the landscape (Archibald et al., 2005) whereby grazers preferentially select recently burned patches as foraging sites (Gureja & Owen-Smith, 2002; Murphy & Bowman, 2007). This short-term concentration of grazing can impede the spread of future fires, suppress grazing intolerant grass species, and concentrate nutrients, leading to the formation of stable

grazing lawns (Fuhlendorf et al., 2009). However, fire characteristics, particularly fire size, can limit the establishment and persistence of grazing lawns. For instance, frequent fires applied across large spatial extents can reduce grazing lawn extent and promote tussock grasslands due to the dispersion of post-fire regrowth and, consequently, grazers, across the landscape. This dispersion allows grasses to escape the ongoing grazing pressure necessary for lawn formation (Archibald et al., 2005; Bowman et al., 2021). In contrast, small scale, patchy fires can concentrate grazing pressure within tall grass areas, initiating a positive feedback loop between fire and grazing and facilitating grazing lawn establishment and persistence (Bond & Archibald, 2003). Therefore, although fire application can be a tool for managers to influence grazing lawn formation in the absence of megagrazers, it is likely only effective under specific burning conditions. While field experiments have provided valuable insights into interactions between grazers and fire (e.g. Archibald & Bond, 2004; Burkepile et al., 2013; Parrini & Owen-Smith, 2010), and grazing lawn establishment following fire (Donaldson et al., 2018), the persistence of grazing lawns once fire application ceases, and the extent of lawn patches created by different fire regimes, are unknown.

Fire-driven changes in grass structure are also not homogenous but vary in horizontal and vertical space due to heterogeneity in fuel connectivity and moisture, creating patchiness in grass biomass and resulting in a mosaic of unburned and burned patches (Cardoso et al., 2022). Horizontal heterogeneity of burned area can lead to variation in forage availability and facilitate grazer coexistence through the spatial partitioning of resources (Cromsigt & Olff, 2006; Fryxell et al., 2005; Owen-Smith, 2004). Similarly, vertical heterogeneity in grass structure caused by fire can facilitate herbivore coexistence by supporting grazers that specialize on different grass heights, often along axes of herbivore body size and muzzle morphology (Arsenault & Owen-Smith, 2008; Sensenig et al., 2010). For example, studies in east and southern African savannas show that small mesoherbivores (e.g. blue wildebeest, *Connochaetes taurinus*, and impala, *Aepyceros melampus*) select more intensively for burnt patches than do larger mesograzers (e.g. plains zebra, *Equus quagga* and buffalo, *Syncerus caffer*), which forage more frequently in taller unburned patches (Burkepile et al., 2016; Sensenig et al., 2010). Similarly, fires can increase the bulk density of grasses in grazing lawns, facilitating increased bite size and rate, and thereby forage intake, by grazers (Drescher et al., 2006; Verweij et al., 2006). However, while it is established that fires can alter the distribution and abundance of herbivores through changes to the grass layer, it remains unclear how different aspects of fire regimes (e.g. fire season and size) impart these modifications and lead to grazing lawn establishment and persistence.

Late dry season fires are generally more intense and complete (Govender et al., 2006) than early dry season fires, which occur when fuel moisture is higher. Thus, late dry season fires could result in larger short grass patches immediately following a burn, potentially driving higher herbivore responses and, subsequently, leading to the formation of persistent grazing lawns. However, the magnet effect following late-season fires might only last for a short period

because the onset of the rainy season improves grass quality over broader extents and disperses grazers (Archibald et al., 2005). In contrast, early dry season fires are patchier, but provide high quality forage for herbivores at a critical time, potentially creating a longer-term magnet effect and thus a higher probability for grazing lawn establishment.

Adequate understanding of how different fire regimes generate variation in the grass layer requires the measurement of grass structure and volume at fine spatial scales over large spatial extents. Existing measurements of grass structure are typically derived through field sampling techniques that are often constrained by limited spatial coverage and an inability to resolve grass volume at varying heights (e.g. Donaldson et al., 2018; Waldram et al., 2008). However, recent advances in miniaturized Light Detection and Ranging (LiDAR) sensors mounted on unoccupied aerial vehicles (UAVs) have enabled the fine-scale characterization of savanna vegetation structure in three-dimensional space. Since UAV-LiDAR can acquire point densities at much higher resolution than traditional airborne LiDAR, the accurate quantification of grass structure over spatially expansive areas is now possible (Boucher et al., 2023).

Here, we use high-resolution UAV-LiDAR data to quantify how variation in fire season and size leads to the formation and persistence of grazing lawns in Kruger National Park (KNP), South Africa. We aimed to: (i) assess whether grazing lawns created through manipulating fire-herbivore feedbacks can persist after the management intervention (i.e. small-scale fires <25 ha in extent) has been withdrawn, (ii) use high-resolution UAV-LiDAR to quantify key short grass habitat parameters (grass height, volume, cover, patch area and spatial continuity) relevant to herbivore preference and (iii) identify the most effective fire regimes for grazing lawn persistence based on the above metrics. We hypothesize that: (1) smaller fires will result in more persistent and continuous short grass patches over time because smaller fires more strongly concentrate grazers, leading to larger grazer feedbacks and prolonged persistence of short grass patches and (2) patches burnt by early dry season fires will have a more homogenous distribution of short grass than late-season fires due to grazers spending a greater proportion of the dry season on early-season burns, driving the formation of grazing lawns.

2 | MATERIALS AND METHODS

2.1 | Study site

We worked in the Satara region (24°22' S, 31°50' E) of KNP (Figure 1a), which is located on basalt geology of relatively low elevation (215 m a.s.l.) and slightly undulating terrain. Mean annual precipitation is 544 mm year⁻¹, falling mostly between October and March (Venter et al., 2003). The vegetation consists of open savanna (woody cover ~10%) with a mosaic of short and tall grass cover (Voysey et al., 2021). The tree community is dominated by *Acacia* (syn. *Vachellia*) *nigrescens*, *Dichrostachys cinerea*, *Scelrocarya berrea*

and *Dalbergia melanoxylon*, while the grass layer consists of mostly *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, *Urochloa mosambicensis* and *Themeda triandra* (Donaldson et al., 2018). Fire is an important determinant of vegetation structure in the region (Donaldson et al., 2018), with an average fire return interval of 3 years (Govender et al., 2006). Most fires occur during the dry season (June–October), and the majority of these fires take place in the late dry season (August–October) (van Wilgen et al., 2022). A diverse range of herbivores are present in high abundance, including grazers (blue wildebeest, plains zebra and buffalo) and mixed feeders such as impala (Burkpile et al., 2016).

2.2 | Experimental design

To measure the effects of fire on short grass dynamics, a large-scale fire-herbivory interaction experiment was established in the Satara landscape in 2013 (Donaldson et al., 2018). Early and late dry season fires were applied at three spatial scales (0.25, 5 and 25 ha), with all experimental fires located within 10 km of each other (Figure 1b). These spatial scales were selected to mirror the three dominant short grass habitats in KNP: termite mounds (Davies et al., 2016), naturally occurring sodic sites (Grant & Scholes, 2006) and expansive grazing lawn systems (Yoganand & Owen-Smith, 2014). Four replicates of controlled early (April/May) and late dry season (October) burns were applied at two spatial scales: 0.25 and 5 ha, and three late dry season burns were applied over 25 ha. Early burns at 25 ha were not performed due to spatial and logistical constraints. Recently unburned areas (hereafter unburned plots), where fires were excluded over the experimental period, of matching size was selected adjacent to each treatment plot for a total of 38 plots: 19 treatment and 19 unburned (Figure 1b,d). Experimental fires were applied in 2013, 2014 and 2015. Fires were not set in 2016 or 2017 due to a severe drought and subsequent lack of grass. All experimental plots were burnt in the late dry season of 2018 and 2019, when the last fires before our sampling, in December 2020, were set. The treatments remained open to herbivores throughout the experiment. Grass height was measured before the start of the experiment in 2013 and ranged between 0.37–0.57 m (Donaldson et al., 2018).

2.3 | LiDAR surveys and data processing

High-resolution airborne LiDAR data were collected across ~1300 ha of the experimental area and adjacent landscape using the Harvard Animal Landscape Observatory (HALO). HALO integrates a high-resolution LiDAR sensor (Riegl VUX-1LR), a thermal camera, and an RGB imaging camera mounted on an UAV (Boucher et al., 2023), which in this study was a Freefly Alta-X. All UAV flights were conducted at 100 m above ground level (AGL) with a flight speed of 8 ms⁻¹. Surveys were conducted in December 2020 (early wet season) when the vegetation was in leaf-on stage, enabling quantification of vegetation structure after a full-growing year since the most

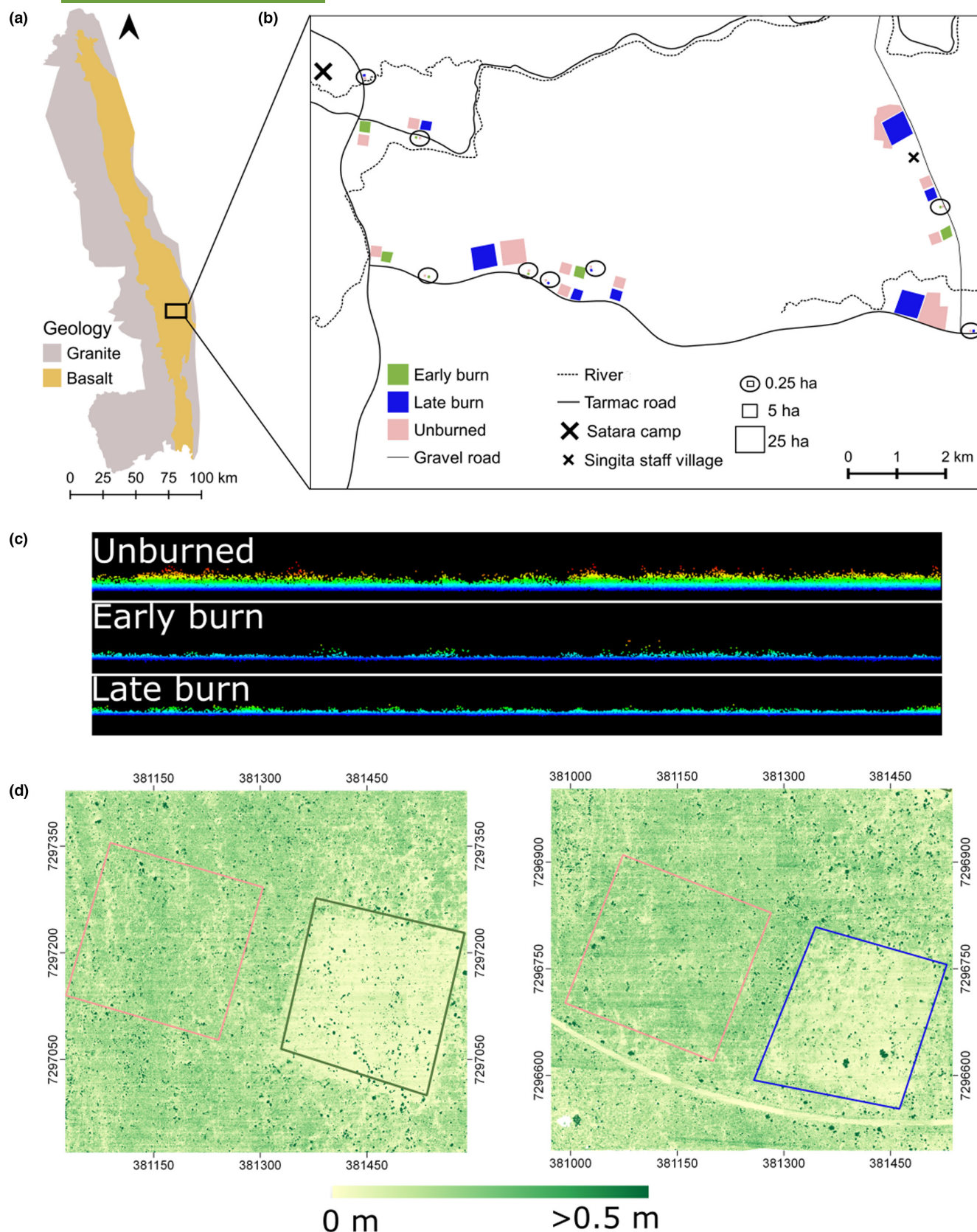


FIGURE 1 (a) Location of the Satara fire-grazer interaction experiment in Kruger National Park, South Africa. (b) Layout of the fire treatment and control plots in the Satara landscape. Experimental fires were applied in the early (May; depicted in green) and late (October; depicted in blue) dry season at three spatial scales: 0.25, 5 and 25 ha. Unburned treatments were selected adjacent to the fire treatment plots and are depicted in pink. (c) Vegetation height profiles of three-dimensional vegetation structure across unburned, early and late dry season fire treatments measured with unoccupied aerial vehicle-Light Detection and Ranging. (d) Grass height (0.25 m spatial resolution) across example fire treatment and control plots, the green polygon indicates an early dry season treatment; the blue polygon a late dry season treatment and the pink polygons unburned treatments.

recent fires (October 2019). LiDAR data were acquired at 600kHz laser pulse repetition rate with flight lines spaced 114m apart to yield 60% side overlap with 110-degree field of view. All UAV flights were conducted in accordance with South African Civil Aviation Authority (SACAA) requirements under a Registered Operating Certificate belonging to Integrated Aerial Systems. A SACAA certified pilot performed all flights, and permission to operate in KNP was obtained from South African National Parks (permit number DAVAB1630) prior to the surveys.

LiDAR data were first denoised to eliminate isolated points, with data from different flightlines then matched by applying heading, roll and fluctuation corrections in the *Terramatch* module of the *Terrasolid* software suite (<https://terrasolid.com>). The matching accuracy for all surveys ranged between 3 and 4 cm, and the average point density after noise removal was 150 points m⁻². The denoised and matched LiDAR data were ground classified and then height normalized with respect to the ground class by calculating the distance of each three-dimensional (3D) point to a triangulated iterative network model of the ground (Figure 1c). Lastly, rasterized canopy height models (CHM) were created by gridding the highest 'z' coordinate among first-return LiDAR points at 0.25m spatial resolution (Figure 1d). Within the CHMs, we randomly selected unburned regions located within 100m of the fire treatments using the *sample* function in R and classified them as unburned. When the randomly selected unburned plot was in a location where short grass structure was deemed to be influenced by drainage lines or gravel roads, we rotated the unburned area in a clockwise direction around the treatment plot until a matching site was found.

2.4 | Assessment of short grass vegetation structure

From the processed LiDAR data, we extracted structural metrics of vertical (grass height, grass cover and grass volume across heights) and horizontal (grass cover, grass volume, short grass patch size and bare ground extent) grass structure. Grass height was measured as the maximum height of the individual CHM pixels at a resolution of 0.25m. To calculate grass cover, we placed a 20×20m (0.04 ha) grid over each of the fire treatment and unburned CHMs. The CHMs were then binary reclassified using the R package *raster* (Hijmans, 2024), where pixels <0.01 and >0.5m in height were classified as 0, and pixels with height values between 0.01 and 0.5m were categorized as 1, representing grass cover. The reclassified CHMs were then expressed as percent grass cover by dividing the number of grass pixels in each grid cell by the total number of pixels within the cell. To quantify resource partitioning produced by the fire treatments, we followed the same procedure but quantified percent grass cover at varying height intervals by systematically adjusting the binary classification heights, thereby calculating grass cover at 0.01, 0.05, 0.1, 0.2, 0.3, 0.4 and 0.5m. We selected a maximum height threshold of 0.5m

because we were focused on the grass layer (rather than woody vegetation), and the mean grass height across the fire treatments and recently unburnt areas was 0.18 and 0.32m, respectively. We also quantified the percentage of bare ground across the treatments by calculating the percentage of pixels <0.01m in height within each plot.

To measure grass volume across the grass height categories, we applied a voxelization-based method on the LiDAR point cloud. First, the LiDAR point clouds were clipped to only include points between 0.01 and 0.5m in height, following which a voxel grid of 5×5×5cm resolution was applied using the *lidR* package in R (Roussel et al., 2020); grass volume was then estimated as the product of the number of occupied (i.e. containing at least one LiDAR point) voxels multiplied by the total voxel volume over each 20×20m grid cell. Next, the voxel grids were divided into six height strata (1–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm and 40–50 cm). We then calculated the sum of all voxel volumes over the 20×20m grid cells separately for each of the six height strata, thereby obtaining height-specific volumetric data from the 3D point clouds. The volume of grass in each height stratum was then divided by the total volume in that column, resulting in a volume proportion for each height stratum. We then calculated the bulk density of the grass layer across the height strata by repeating the same procedure but including the number of points in each voxel (rather than a binary classification of a voxel being occupied by points or not) to represent bulk density.

To quantify grazing lawn extent across the treatment and unburned plots, we used the *clumps* function in the *raster* R package (Hijmans, 2024) to identify short grass patches in the CHMs. Short grass patches were defined as clumps where there were at least 4×4 (i.e. 16) neighbouring 0.25m pixels (i.e. a rook's scheme) of grass height between 0.02 (a more conservative height threshold to ensure that we did not conflate bare ground with grass cover) and 0.05m (Figure 2). We then derived metrics of patch size (area) and shape (perimeter to area ratio) for each clump using the *landscape-metrics* package in R (Hesselbarth et al., 2019). Finally, we computed the radius of each short grass patch as a proxy for visibility for herbivores by calculating the mean distance between the centroid and patch edge vertices using Pythagorean theorem in R. We used vertices spaced at least 1.5m apart for computational efficiency.

2.5 | Statistical analyses

We tested differences in grass cover, volume and patch size across the treatments and plot sizes using a Kruskal–Wallis and Dunn's post hoc comparison test (Dunn, 1961). We also calculated the effect size of the Kruskal–Wallis test (Kotrlík & Williams, 2003) based on the *H*-statistic to determine the percentage of variance in the vegetation metrics explained by the treatment effect using the R package *rstatix* (Kassambara, 2020). The *H*-statistic was interpreted as follows: values >0.01 but <0.06 (small effect), >0.06 but <0.14 (moderate effect) and ≥0.14 (large effect). We used kernel density estimation

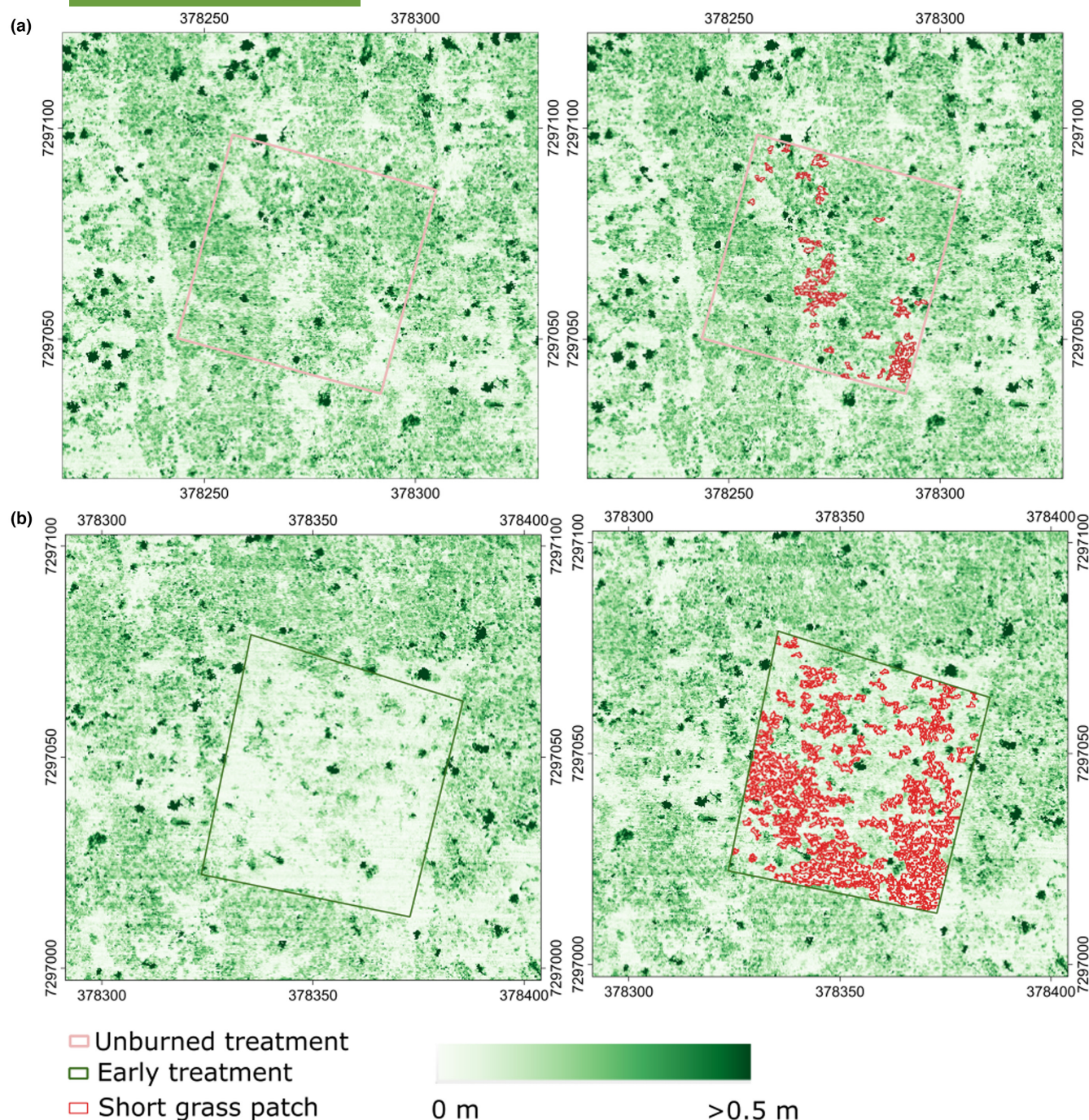


FIGURE 2 An example of short grass (grass height ≤ 5 cm) patch delineation from the canopy height models (spatial resolution 0.25 m) across (a) unburned and (b) early dry season fire treatments in the Satara fire-grazer interaction experiment in Kruger National Park, South Africa. Left hand panels depict original canopy height models while delineated short grass patches are shown as red polygons in the right-hand panel.

(plotted in the R package *ggplot2*, R Core Team, 2021) to compare the distribution of grass height and short grass patch sizes across the fire treatments.

To evaluate the spatial continuity of short grasses patches, we constructed semivariograms in the *gstat* R package (Pebesma & Graeler, 2023). Empirical semivariograms were derived across the fire treatment and unburned plots for grass heights between 0.02 and 0.05 cm using a lag distance of 1 m and 6000 height values.

Following conventional practice, a theoretical model was then constructed using a weighted least squares approach applied to each empirical semivariogram (Cressie, 2015). The spherical model was found to be the most appropriate and was used to derive the semivariogram range (the distance at which points are effectively uncorrelated, that is have no spatial dependence). The semivariogram range for each fire treatment was compared to the adjacent unburned plot using an unpaired two-sample t-test.

3 | RESULTS

3.1 | Grass height

The distribution of grass height varied substantially among the treatments, demonstrating the strong effect of fire in shaping the grass layer ($\eta^2[H] = 0.16$, $p < 0.001$) (Figure 3). Grass height was 49% lower in the burnt plots than the unburned plots, with a higher density of short grass pixels in the early dry season fire treatment plots compared with the late dry season fire treatments (kernel density estimate: unburned-5.8, early dry-15.6, late dry-12.5). Pairwise Dunn's test comparisons revealed significant differences between unburned and both early and late dry season fire treatments, while no significant difference was observed between early and late dry season fire treatments (Unburned-early dry: z -value=11.8, $p < 0.001$; Unburned-late dry: z -value=7.93, $p < 0.001$; early-late dry: z -value=-0.696, $p = 1$). Moreover, the distribution of short grass did not differ across the fire treatment sizes ($\eta^2[H] = 0.0003$, $p = 0.09$).

3.2 | Grass volume and bulk density

The volume proportion of the grass layer across the vertical height increments differed significantly between fire treatments and unburned plots, with 77% more grass volume between 1 and 10 cm in height in the fire treatments (mean volume proportion: Unburned-0.18, fire treatments-0.334) (Figure 4a). The difference in the volume proportion between unburned and fire treatments was greatest for the 1–5 cm height category (0.24 and 0.23 for early and late dry season treatments, respectively), with a large effect size ($\eta^2[H] = 0.61$, $p < 0.001$) (Figure 4b,c). In contrast, for grass height

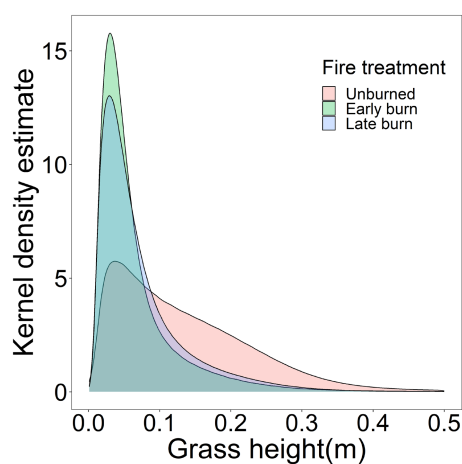


FIGURE 3 Kernel density plots of grass height derived from unoccupied aerial vehicle-Light Detection and Ranging data across fire treatment and control plots in the Satara fire-grazer interaction experiment in Kruger National Park, South Africa. Variation in grass height represents resource partitioning among herbivores because different grazers utilize different grass heights.

intervals >10 cm, unburned plots had greater grass volume than fire treatments, with the largest difference in volume proportion being in the 20–30 cm height category ($\eta^2[H] = 0.70$, $p < 0.01$), followed by a gradual decline in volume proportion differences with increasing height category (Figure 4a–c). Pairwise Dunn's test comparisons revealed significant differences in grass volume proportions between unburned and early dry season fires, and unburned and late dry season fire treatments for all height categories apart from the 5–10 cm height category. In contrast, grass volume proportion across height classes did not differ across fire treatment sizes ($\eta^2[H] = 0.01$, $p = 0.96$) (Figure 4b,c). Results for the bulk density measurements were qualitatively similar to those of volume estimates (see Figure S4).

3.3 | Grass cover

Fire treatment also influenced the extent of short grass cover, with early and late dry season fire treatment plots containing 2.78 and 2.45 times more short grass cover, respectively, than unburned plots (Figure 4d). Significantly more grass cover was recorded in the fire treatments up to a 10 cm height threshold (5 cm: $p < 0.001$, $\eta^2[H] = 0.52$; 10 cm: $p < 0.01$, $\eta^2[H] = 0.46$), while at taller height thresholds, grass cover was greater in the unburned plots (20 cm: $\eta^2[H] = 0.35$; 30 cm: $\eta^2[H] = 0.50$; 40 cm: $\eta^2[H] = 0.58$; 50 cm: $\eta^2[H] = 0.59$; $p < 0.01$) (Figure 4e,f). Pairwise comparison Dunn's tests revealed that the distribution of grass cover varied significantly across unburned plots and early dry season fires, unburned plots and late dry season fires, and late and early dry season fire treatments ($p < 0.01$ for all comparisons). Short grass cover across fire treatments of different sizes was significantly different, but with a negligible effect size ($\eta^2[H] = 0.0003$, $p < 0.01$) (Figure 4e,f).

Bare ground cover in all plots was low, but consistently higher in fire treatments (season and size) than in the unburned treatments, with a mean bare ground cover of 1.5% and 0.7% in fire treatments and unburned treatments, respectively (Figure S1).

3.4 | Short grass patch size

The delineation of short grass patches revealed significant differences in short grass patch sizes between all fire seasons and sizes (Figure 5; $p < 0.001$ for all treatment group comparisons except between early and late dry season fires at 0.25 ha where $p = 0.87$). Short grass patches were consistently smaller in the unburned plots, irrespective of plot size, while the largest short grass patches were observed in the early dry season fire treatments at both the 0.25 and 5 ha fire treatment scales (Figure 5a,b). Late dry season fire treatments, especially at the 5 ha treatment size, had significantly smaller short grass patches (mean patch size: 11.02 m²; $p < 0.01$) than early dry season fire treatments (mean patch size: 16.28 m²). Unburned plots also had a higher proportion of small patches than early and late dry season fire treatments across all spatial scales (Figure 5d–f). Short

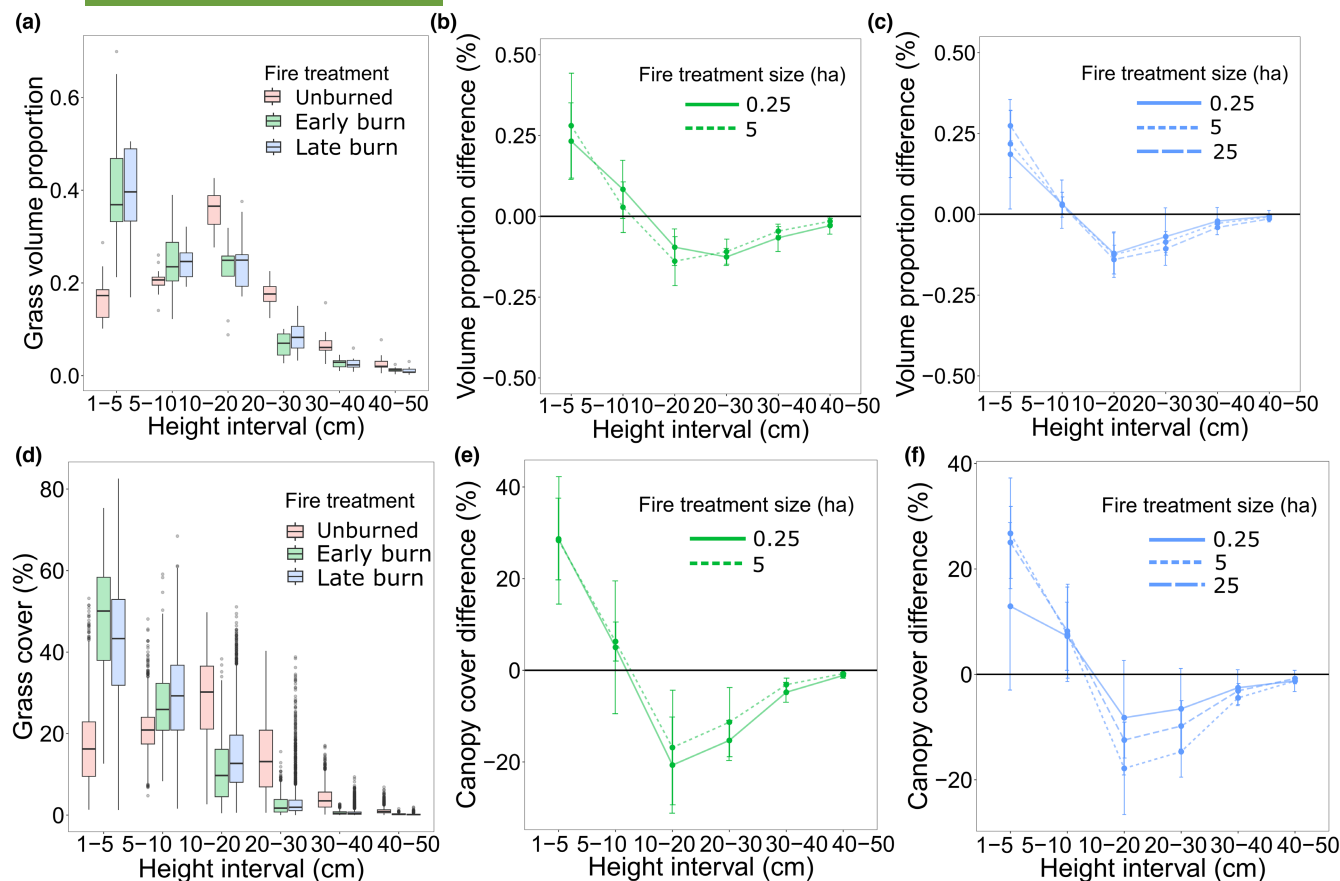


FIGURE 4 Available forage quantity for grazers depicted as (a) the volume proportion of Light Detection and Ranging points in vertical bins and (d) grass cover across fire treatment plots of the Satara fire-grazing interaction experiment in Kruger National Park, South Africa. Boxplots represent data from all treatment sizes (0.25, 5 and 25 ha) across height intervals. (b, c) Percentage volume differences between (b) early dry season and control treatments and (c) late dry season and control treatments across treatment sizes. (e, f) Percentage cover differences between (e) early dry season and control treatments and (f) late dry season and control treatments across treatment sizes. Positive differences indicate the presence of more grass (volume or cover) in the fire treatments, whereas negative differences represent more grass in the control treatments. Results for grass bulk density are shown in [Figure S4](#).

grass patch radii were also significantly longer in the fire treatment plots than the unburned treatment plots across all treatment sizes ($p > 0.01$) ([Figure S3](#)).

3.5 | Spatial continuity of short grass patches

The semivariogram analysis revealed varied levels of spatial heterogeneity across the fire and unburned treatments ([Figure 6](#)). Irrespective of treatment size, unburned plots and late dry season fire treatments exhibited the highest variability in short grass height (semivariance $\gamma(h) = 0.00050$ – 0.00055), whereas the lowest spatial variability was recorded in the early dry season fire treatments (semivariance $\gamma(h) = 0.00040$ – 0.00045), indicating a more homogeneous short grass layer in these treatments. For the fire treatments, the semivariograms levelled off at higher ranges than unburned plots, except for the 25 ha spatial scale where the late dry season treatment semivariograms levelled off at lower ranges ([Figures S5](#) and [S6](#)). The semivariance of short grass patches between fire treatments

differed significantly with treatment size, but with a negligible effect size ($\eta^2[H] = 0.027$, $p < 0.01$).

4 | DISCUSSION

Our results revealed that the application of small-scale fires (<25 ha) can lead to grazing lawn establishment and that these lawns can persist in the landscape at least 1 year after the cessation of fire. Fire treatments had almost four times more short grass area relative to recently unburned parts of the landscape, and 15%–40% more short grass cover across height classes of 1–5 cm (40% more), 5–10 cm (25%–29%) and 10–20 cm (15%) ([Figure 4d](#)). Although both early and late dry season fires had higher short grass cover than unburned treatments, early dry season fires were especially influential for the shortest (1–5 cm) height class ([Figures 3](#) and [4d](#)). Early dry season fire treatments also exhibited a more homogeneous distribution of short grass patches relative to late dry season fires and unburned sites, as evidenced by the

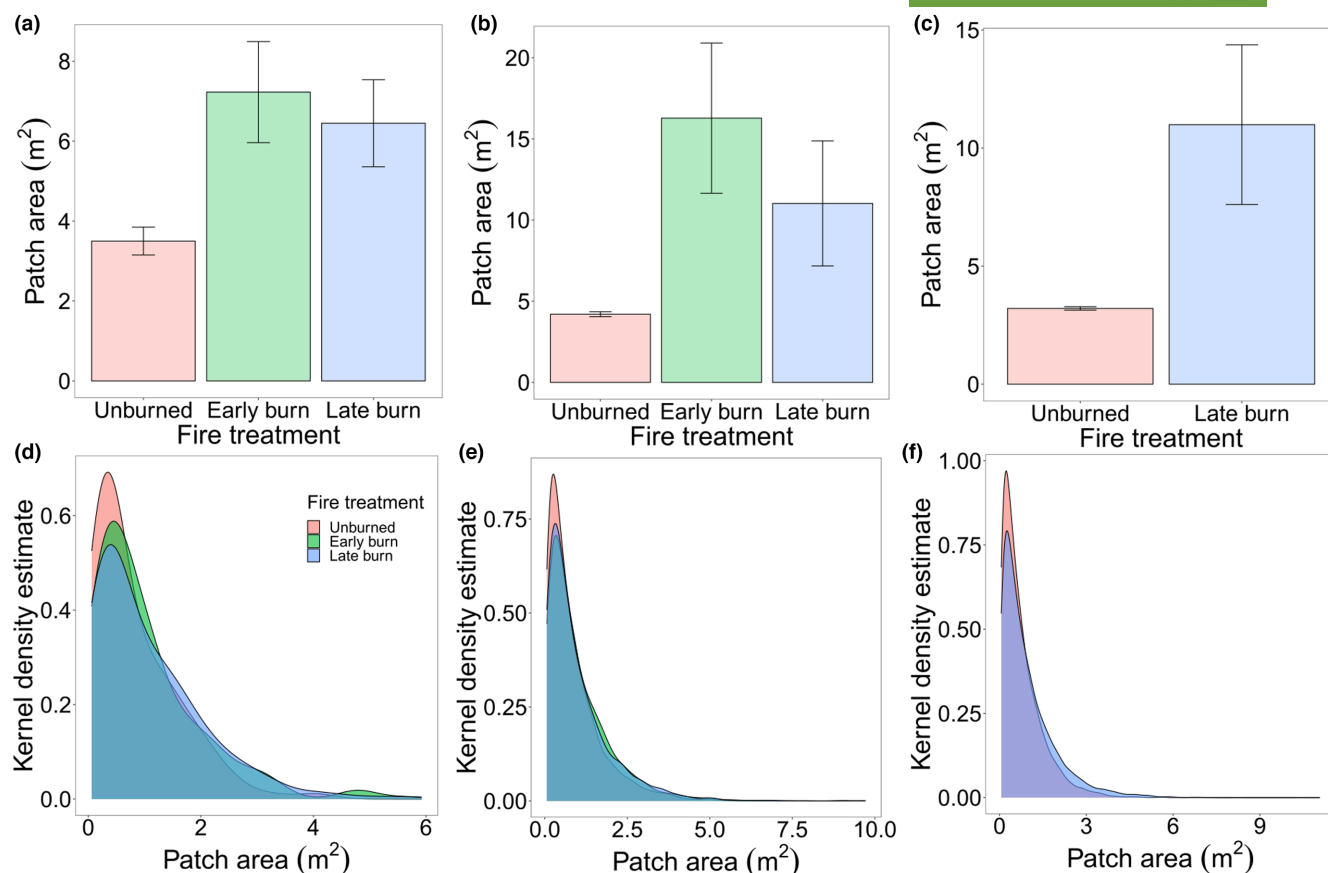


FIGURE 5 Spatial resource partitioning indicated by short grass patch area and size. (a–c) The area of short grass patches (grass height ≤ 5 cm) in fire treatments and control plots of varying sizes: (a) 0.25 ha, (b) 5 ha and (c) 25 ha. Error bars indicate standard errors. (d, e) Kernel density distribution of short grass patch size (m²), log transformed in fire treatments across varying treatment sizes: (d) 0.25 ha, (e) 5 ha and (f) 25 ha. Results for grass height ≤ 10 cm are shown in [Figure S2](#).

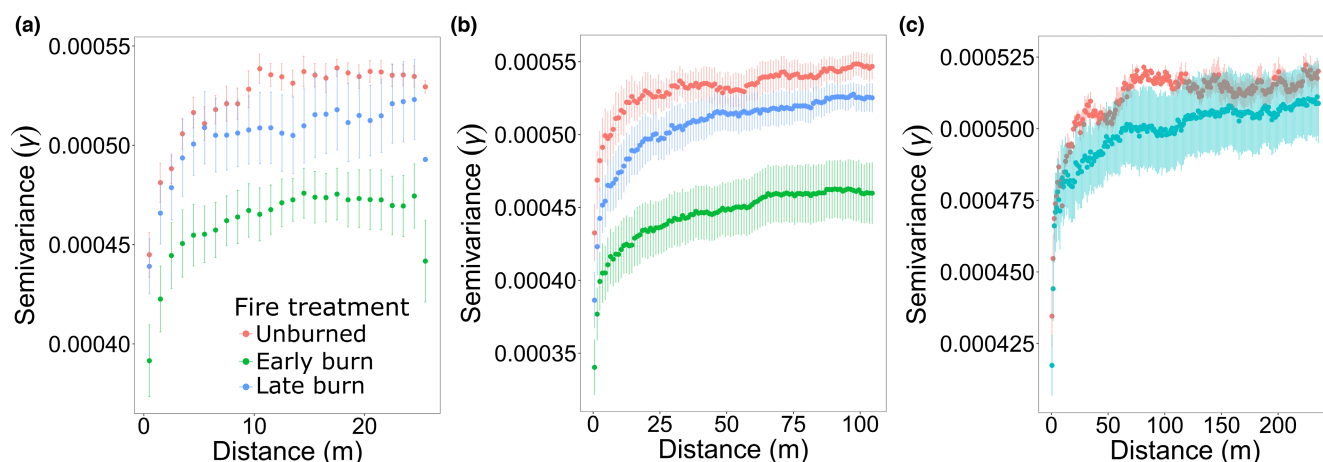


FIGURE 6 Semivariograms of grass height across fire treatments and control plots of varying size: (a) 0.25 ha, (b) 5 ha and (c) 25 ha. Error bars represent standard error. Across all plot sizes, the fire treatments exhibited lower variance in grass height compared with the unburned plots, indicating a more uniform distribution of short grass in the fire treatment plots.

lower spatial variability in grass height in the early dry season fire treatments ([Figure 6](#)). The high-resolution of our LiDAR measurements was also able to demonstrate that the volume (i.e. bulk density) of short grass responds strongly to fire: grass volume below

20 cm in height was significantly greater in both early and late dry season fires ([Figure 4a](#); [Figure S4](#)).

Although grazing lawns were present on all fire treatments, fire treatment size (0.25, 5 and 25 ha) had a negligible influence on short

grass structure, in contrast with our first hypothesis. In line with our second hypothesis, we found that early dry season fires most strongly promoted short grass cover in the shortest height class (1–5 cm), compared with late dry season fires where there was more short grass cover in taller height classes (5–10 cm and 10–20 cm). These differences between fire seasons can possibly be explained by grazer aggregation patterns. Post-fire green flush of grasses following early dry season fires will attract grazers during a time when most grasses in the landscape are curing and becoming less attractive to herbivores, leading to a high concentration of grazers over a longer period of time (Figure 7). This increased grazing then promotes the growth of nutrient-rich lawn grass species (Coetsee et al., 2011; Stock et al., 2010), which, together with improved visibility (i.e. lowering predation risk) (Burkepile et al., 2013; Sinclair et al., 2003), keeps grazers on these patches throughout the dry season, maintaining short grass cover. Conversely, although herbivores are under maximal nutritional stress in the late dry season (Illius & O'Connor, 2000), the Spring rains occur shortly after the late dry season fires, leading to a general greening of grasses throughout the landscape. Thus, grazers

likely concentrate on late dry season burns for a shorter period each year, allowing grass to regrow to a taller height (Figure 7).

Our finding that early dry season fires are more influential for grazing lawn establishment than late dry season fires differs from initial assessments, performed in 2015, of short grass structure following the fire treatments, when a complete switch from bunch grasses to lawn grasses was documented (Donaldson et al., 2018). When comparing our short grass cover estimates with these earlier ones, we observed a 29% decline in short grass cover across the late dry season fire treatments, and a 47% increase in short grass cover in the early dry season fire treatments. These differences could be attributed to the initial effects of frequent burning in the late dry season treatments that led to the complete removal of standing grass biomass in the first few years of the experiment compared to early dry season burns where biomass consumption by fires was patchier (Donaldson et al., 2018). However, repeated extended grazing on early dry season burns throughout the dry season seemingly resulted in more persistent structural changes in the grass layer, as observed in our study.

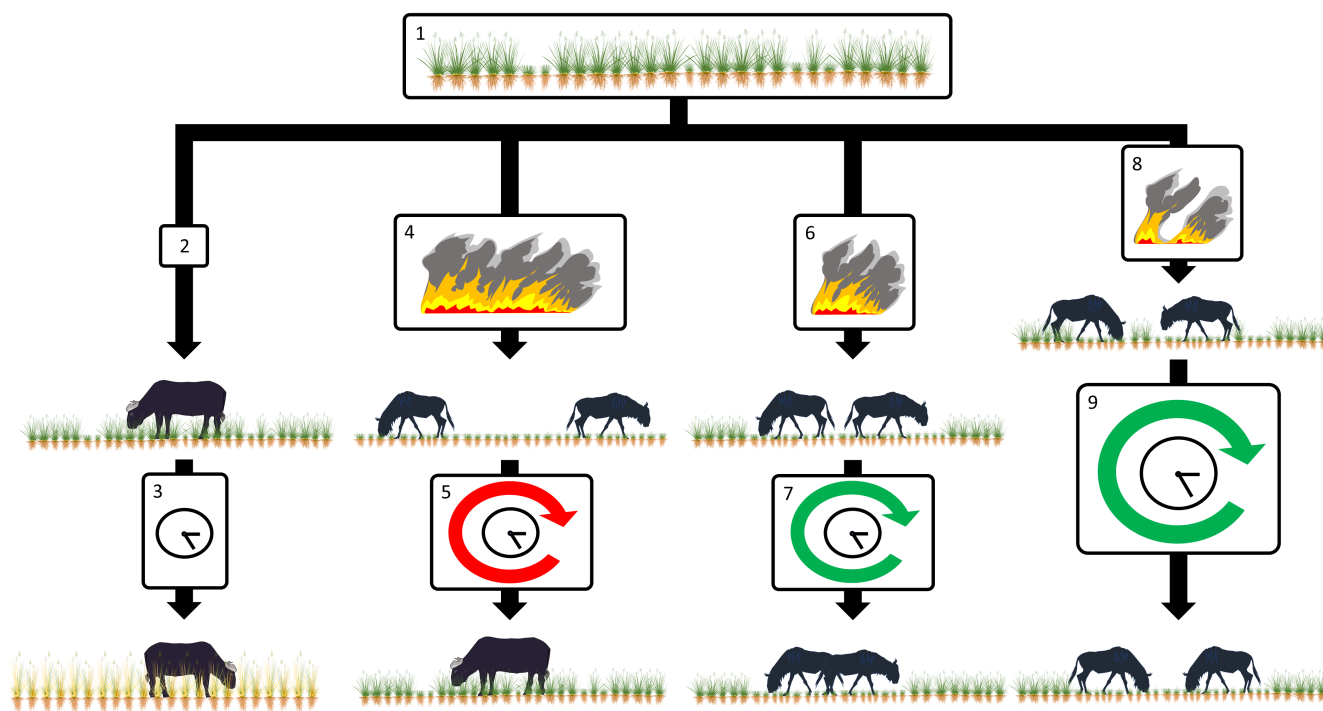


FIGURE 7 Conceptual framework of the effects of fire size and season on herbivore responses and feedbacks in savannas dominated by tall-tussock grasses. (1) In the absence of fire, grass accumulates over the season and (2) favours grazers that feed optimally on tall grass such as buffalo (*Syncerus caffer*), before (3) senescing with time and losing nutritional value. Alternatively, (4) large seasonal fires consume standing grass biomass and stimulate fresh, high-nutrient regrowth that attracts grazers such as blue wildebeest (*Connochaetes taurinus*) that feed optimally on short grass. Following these large fires, grazers are dispersed over broad burned areas and do not maintain grass in a short state, with (5) grass regrowing and 'escaping' to grass heights that again favour species such as buffalo; feedbacks between short grass specialists and the grass layer are not established. In contrast, (6) smaller, late-season fires create the same highly nutritious regrowth as in (4), but concentrate grazing in small patches where grazer densities become high enough to limit grass regrowth and (7) establish feedbacks that maintain short grass patches throughout the season and encourage repeat grazing by short grass specialists. (8) Early-season fires are patchier than late-season fires due to the higher fuel moisture content in the grass layer and result in patchier distributions of short grass. However, the timing of early burns means that herbivores concentrate on burnt patches for a longer period of time and (9) maintain short grass patches more effectively, ultimately generating stronger grazer-grass feedbacks than similarly sized late-season fires.

The establishment of grazing lawns on the fire treatments, and especially on the early dry season fire treatments, led to heterogeneity in the spatial and vertical grass structure across the Satara landscape, which is crucial for the maintenance of diverse mammalian grazer communities that partition resources by feeding at different grass heights (Table S1) (Arsenault & Owen-Smith, 2008; Cromsigt & Olff, 2006). Our study demonstrates that small-scale (<25 ha) burns can drive increased local grazing and promote persistent spatial heterogeneity in grass structure to the benefit of short grass specialist grazers. For example, fire-grazer interactions on early and late dry season burns led to a significant (49%) increase in short grass cover and forage availability within the optimal vertical foraging range (<10 cm) for wildebeest (Murray & Brown, 1993; Wilmshurst et al., 2000). In contrast, forage availability within the preferred vertical foraging range for buffalo (20–30 cm, Arsenault & Owen-Smith, 2008) decreased from 29% in the unburned parts of the landscape to just 14% within the fire treatments. Declining populations of megagrazers (e.g. white rhino) in KNP and elsewhere (Nhleko et al., 2022) are likely to lead to the homogenization of grassland structure and an increase in tall grass (Cromsigt & te Beest, 2014), potentially limiting populations of short grass specialists. While other grazers consume short grass, megagrazers are uniquely capable of creating grazing lawns (Voysey et al., 2023; Waldram et al., 2008). Our findings suggest that the application of small-scale fires, especially in the early dry season, could alleviate some of this homogenization and serve as an important management tool for the maintenance of diverse herbivore communities.

Along with facilitating the coexistence of different herbivore communities, larger short grass patches could also modify the feeding behaviour, movement and space-use patterns of short grass specialists (Gaynor et al., 2019; Valeix et al., 2009), that are known to respond to short grass patch size (Luhdo, 2016; Wirsing et al., 2010). Herbivores spend more time foraging and less time on vigilance in larger short grass patches due to them being able to more easily detect predators when in larger patches (Luhdo, 2016). Our results demonstrate that small-scale fires applied in the early dry season increase short grass patch sizes and could enable herbivores to feed more efficiently: we measured patch radii of up to of 110–150 m and 10–25 m for 5 and 0.25 ha early dry season fire plots, respectively (Table S1; Figure S3). Patches of this size likely provide significant benefits for small-bodied herbivores that can reduce vigilance costs, allowing for more efficient foraging (Creel et al., 2014; Dröge et al., 2017).

Our results also demonstrate the utility of UAV-LiDAR for characterizing the grass layer. Although airplane-based LiDAR datasets have been previously used to characterize 3D woody vegetation structure in savanna ecosystems (Davies & Asner, 2014), the characterization of the herbaceous layer has been largely unachievable, mainly due to insufficient point density. In contrast, the high point density (>150 points m⁻²) of our LiDAR dataset enabled us to measure the 3D vertical structure of the grass layer, stratify

grass volume across vertical heights and quantify spatial patterns of short grass. These technological advances could be applied to other questions related to savanna grass structure, such as fire spread models or herbivore effects on vegetation structure beyond woody plants.

4.1 | Implications for management

In recent years, a decline in forage quality within savanna landscapes (including Satara) has been observed, potentially due to increased fire frequency (Trollope et al., 2014; van Wilgen et al., 2014) and the cessation of herbivore migrations (Fynn & Bonyongo, 2011). These shifts in grass communities have led to concerns about the availability of a diverse landscape of forage quality and the ability of many savanna ecosystems to maintain diverse herbivore populations (Venter et al., 2008). Accordingly, savanna managers often adopt adaptive fire management policies to increase variability in the grass layer, including a reduction in the intensity, frequency and extent of fires (van Wilgen et al., 2014). However, comprehensive information on the role of fires in creating resource heterogeneity along horizontal and vertical axes for grazer populations has been limited. Our results suggest that the application of small-scale fires, especially during the early dry season, can create resource heterogeneity and the persistence of short grass patches beyond the cessation of the management intervention. However, we recommend that managers consider these fire effects within the context of individual grazer species. For example, if the goal is to promote habitat for short grass specialists such as white rhino or blue wildebeest, early dry season fires can be used to increase short grass cover. But if the goal is to create variation in the grass layer for a diversity of grazers, some areas should be left unburnt for longer periods (or late dry season fires applied) to maintain patches of taller grass cover.

As valuable as grazing lawns are to savanna ecosystems, there is concern over an increase in bare ground leading to soil erosion on lawns (Anderson et al., 2007; Bestelmeyer, 2006). However, in our study, we found bare ground patches in the fire treatment plots to be very small, covering just 4–6 m² (1%–1.5%) at a 20 × 20 m grid scale (Figure S1); in contrast to other recent analyses where frequent grazing led to significant increases in the extent of bare ground (Donaldson et al., 2018; Hempson et al., 2022). Our comparatively low measurements of bare ground, including comparisons made to field surveys of the same sites in 2015 (Donaldson et al., 2018), could result from colonization over time by laterally spreading grasses capable of growing under high grazer pressure. Alternatively, the low bare ground cover could have resulted from above-average precipitation in the Satara landscape during the 2018–2019 and 2019–2020 wet seasons (SANParks data), with increased moisture availability facilitating revegetation of bare patches. It is also worth noting that LiDAR measurements measure aerial grass cover rather than basal cover that field surveys tend to focus on, thereby likely classifying

patches with even slight grass cover as being vegetated. Such differences potentially prohibit direct comparisons between LiDAR and field techniques and require further investigation. Nevertheless, our measurements of bare ground cover are well below thresholds of concern for soil erosion, estimated at around 20% bare ground (Trollope et al., 1989), meaning that even if they are underestimates of bare ground cover, bare ground in our study system is still likely well below concerning levels.

Beyond managing savanna fires for mammalian herbivores, there is much interest in manipulating fire regimes to reduce carbon emissions and earn carbon offsets. However, these proposals need to be considered within the context of the important ecological role fire plays in savanna ecosystems, and manipulating burning to reduce emissions can have negative consequences for biodiversity (Corey et al., 2020). Although managers have multiple competing objectives related to fire management, our results suggest that in situations where the goal is to increase heterogeneity in the grass layer and/or the extent of short grass, small early dry season fires should be implemented. Such early-season burns also have lower carbon emissions (Lipsett-Moore et al., 2018), suggesting that in this case we can achieve both lower emissions and biodiversity benefits.

AUTHOR CONTRIBUTIONS

All authors (Jenia Singh, Jason E. Donaldson, Sally Archibald, Catherine L. Parr, Michael D. Voysey and Andrew B. Davies) conceived the study design; Andrew B. Davies and Michael D. Voysey conducted the UAV data acquisitions; Jenia Singh processed the remote sensing data, performed the data analysis and wrote the first draft. All authors interpreted the results and contributed revisions.

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CONFLICT OF INTEREST STATEMENT

Catherine Parr is an Associate Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the data available on the Dryad Digital Repository via <https://doi.org/10.5061/dryad.z612jm6kc> (Singh et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Bare ground cover at a 20×20m spatial scale across varying treatment sizes: (a) 0.25 ha, (b) 5 ha, and (c) 25 ha.

Figure S2. Spatial resource partitioning indicated by short grass patch area and size.

Figure S3. Radius of short grass patches at a grass height threshold of 5 cm across varying treatment sizes: (a) 0.25 ha, (b) 5 ha, and (c) 25 ha.

Figure S4. Available forage quantity for grazers depicted as the density of LiDAR points in vertical bins (a proxy for bulk density) across fire treatment plots of the Satara fire-grazing experiment of Kruger National Park, South Africa.

Figure S5. Semivariogram range estimates for early dry season and recently unburnt control (fire exclusion) plots across (a) 0.25 ha and (b) 5 ha sizes.

Figure S6. Semivariogram range estimates for late dry season and recently unburnt control (fire exclusion) plots across (a) 0.25 ha, (b) 5 ha and (c) 25 ha sizes.

Table S1. Summary of short grass structural metrics used in this study and their ecological implications for herbivores.

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